THE WESTERN BALSAM BARK BEETLE,

DRYOCOETES CONFUSUS SWAINE:

IMPACT AND SEMIOCHEMICAL-BASED MANAGEMENT.

by

Arthur J. Stock

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Name: **ARTHUR JOSEPH STOCK**

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Examining Committee:

Chairman: Dr. D.L. Baillie

Dr. J.H. Borden, Professor,
Dept. Biological Sciences, SFU

Dr. R. Brooke, Associate Professor,
Dept. Biological Sciences, SFU

Dr. L. Safranyik, Research Scientist,
Canadian Forestry Service, Victoria, B.C.

Dr. K. Lertzman, Associate Professor,
School of Resource & Environmental Management
Program, SFU, Public Examiner

Dr. J.A. McLean, Professor, Faculty of
Forestry, UBC, Public Examiner

Dr. T.D. Paine, Professor, Dept. Entomology,
U. of California, Riverside, U.S.A.
External Examiner

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Auth

(signature)

ARTHUR J. STOCK

(name)

15 AUG 1991

(date)

Abstract

Aerial and ground surveys disclosed approximately 28,800 ha of infestation by the western balsam bark beetle, *Dryocoetes confusus* Swaine, in mature forests of subalpine fir, *Abies lasiocarpa* (Hook.) Nutt. in north-central British Columbia. *D. confusus* caused mortality was estimated to be 1 m^3/ha/yr, primarily concentrated on the largest and most valuable trees. Mortality was marginally within BC Forest Service acceptable loss estimates. Field experiments demonstrated that *D. confusus* responded optimally to 8-unit multiple funnel traps baited with mixtures of (+)- and (-) *exo*-brevicomin. *exo*-Brevicomin released at 0.8 mg/24 h induced mass attack on 80% of baited trees. Baiting of more than one tree in a spot increased attack intensity on baited trees. Within-stand seasonal flight patterns of *D. confusus* were monitored for three years in north-central British Columbia using multiple funnel traps baited with (±)-*exo*-brevicomin. There were two major flight periods per year, the first commencing in mid- to late June, and the second in mid- to late August. The second flight was composed primarily of females, probably reemerged parent adults. Very little flight occurred at temperatures $< 15^0$ C. Traps placed 6 m above ground caught four times as many beetles as traps placed 2 m above ground. Containment and concentration of *D. confusus* infestations was demonstrated when *exo*-brevicomin released at 0.4 mg/24 h was applied to trees on a 50 m grid over nine ha blocks, or released at 0.8 mg/24 h/tree and applied to two trees at each 50 m centre over the central four ha of 16 ha blocks. Within-stand distribution of attacked trees was highly aggregated (Clark-Evans test). Treatments with *exo*-brevicomin at two trees/spot concentrated 89 % of newly mass-attacked trees within 10 m of baited trees. Laboratory and field experiments demonstrated that (+)-*endo*-brevicomin is an antiaggregation pheromone for *D. confusus*, and that the (-) enantiomer was benign. (+)-*endo*-Brevicomin prevented attack on subalpine fir trees baited with *exo*-brevicomin, while (±)-*endo*-

brevicomin reduced attack on felled trees by up to 93 %. Infestations in 1 ha blocks of standing forests treated at 10 m centres with (±)-*endo*-brevicomin decreased by 30%, even when four trees at 50 m centres were baited with (±)-*exo*-brevicomin.

Dedication

Dedicated to my parents,

Lloyd Joseph and Yvette Marie

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Preface

For brevity and clarity, I have used common names of insects, trees, and chemicals throughout the body of the thesis. Insect and tree specific names with authorities, and proper chemical IUPAC names are listed in Appendix I.

Chapter 2.0 is based on:

Stock, A.J. 1986. Assessment of pest damage to subalpine fir stands in the Bulkley TSA. Final report submitted to the British Columbia Ministry of Forests through the Forest Resource Development Aggreement. BC Ministry of Forests, Smithers, B.C.

Chapter 3.2 has been published as:

Stock, A.J., J.H. Borden, and T.L. Pratt. 1990. *Endo*-brevicomin: an antiaggregation pheromone for the western balsam bark beetle, *Dryocoetes confusus* Swaine (Coleoptera: Scolytidae). Can. Ent. 122: 935-940.

THE WESTERN BALSAM BARK BEETLE, *DRYOCOETES CONFUSUS* SWAINE: IMPACT AND SEMIOCHEMICAL-BASED MANAGEMENT

1. INTRODUCTION

1.1 BIOLOGY AND IMPORTANCE OF *DRYOCOETES CONFUSUS*

The western balsam bark beetle, *Dryocoetes confusus* Swaine, occurs throughout the range of its host, subalpine fir, *Abies lasiocarpa* (Hook.) Nutt. (Hopping 1946; Bright 1963). Subalpine fir has the greatest latitudinal range of North American *Abies* spp., occuring throughout western North America from British Columbia and Alberta to New Mexico (Fowells 1965). Subalpine forests occupy the highest forest environments in the Rocky Mountains, with a climate characterised by cool summers, very cold winters with heavy snowfall, and generally high humidity (Sudworth 1916), although extreme moisture deficits do occur (Alexander 1987). Subalpine fir and its major associate Engelmann spruce are intolerant of high temperatures or deficient moisture (Alexander 1987), and display extreme intolerance to fire damage (Fischer and Brindley 1987). These forests do not appear to be very susceptible to catastrophic disturbances by wind or fire. Available data suggest that old-growth subalpine spruce-fir stands routinely reach ages of ≥ 300 years, and the interval between fires may be as great as 400 years (Kiil 1971; Hanley *et al.* 1975; Alexander 1985). Subalpine fir generally occurs at higher densities than spruce in old-growth stands, but spruce is of greater diameter, and often accounts for 70 - 90 % of stand basal area (Kiil 1971; Hanley *et al.* 1975; Alexander 1985).

The subalpine forests of British Columbia cover large areas of the interior of the province. The main constituents of this forest are lodgepole pine, Engelmann spruce, white spruce, and subalpine fir. Engelmann spruce is predominant in southern British Columbia, but gives way to white spruce in the northern third of the province (Whitford and Craig 1918).

Interior subalpine spruce-fir forests are an important component of the B.C. wood industry. True firs in interior British Columbia represent 13 % of total provincial gross mature standing volume (Council of Forest Industries of British Columbia 1989). In 1967, subalpine fir represented 3 % of the total B.C. wood production volume, and in 1977 and 1988, 6 %, probably reflecting increased utilization due to expanding cut volumes, and decreasing availablility of other woods (British Columbia Forest Service 1968, 1978; Council of Forest Industries of British Columbia 1989). The potential for large scale volume loss becomes increasingly important as the subalpine forest is more heavily utilized. Because harvesting and intensive forest management in western Canada, and particularly in B.C., are moving into high-elevation spruce-fir stands, the impact of *D. confusus* is of increasing concern. In other areas, e.g. the western U.S.A., *D. confusus* infestations threaten the integrity of protection forests maintained for hydrologic and aesthetic imperatives (Dave Holland, pers. comm.[1]). In both situations there is a demand for reduced infestation levels.

Dryocoetes confusus was first described by Swaine (1912). Mathers (1931) described a two-year life cycle for beetles observed in B.C., but Bright (1963) suggests that the life cycle is completed in one year or less in the western and southwestern United States. Some further biological observations were made by Stock (1981). The entomopathogen, *Beauvaria bassiana* (Bals.) Vuill., has been found infecting *D. confusus*, but the role of the disease in the population dynamics of *D. confusus* is unknown (Whitney *et al.* 1984).

D. confusus appears to be the only member of its genus capable of causing economic loss by killing healthy trees (Bright 1963), and is the most destructive insect pest of subalpine fir in British Columbia. Tree mortality caused by *D. confusus* was noted by Swaine (1933), and Hopping (1946) considered it a serious problem. The impact of *D.*

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1. USDA Forest Service, Forest Pest Management, Ogden, Utah.

confusus has been considerable in British Columbia, where records show that the beetle killed trees amounting to 15 million m^3 of timber between 1948-1975 (Stock 1981).

Like many other aggressive scolytid species (Coulson 1979; Whitney 1982), *D. confusus* is symbiotically associated with a lethally pathogenic "blue-stain" fungus, *Ceratocystis dryocoetidis* (Kendrick and Molnar) (Molnar 1965; Kendrick and Molnar 1965), which it introduces into living trees during the initial phases of attack. Thoracic mycangia, special repositories for transporting and maintaining fungi, have been identified on *D. confusus* (Farris 1969). Blue-stain fungi can also be carried as a contaminant of the beetle exo-skeleton, or can carried by phoretic mites (Bridges and Moser 1983), which are common on emerging *D. confusus* (Stock 1981). It has been estimated that *C. dryocoetidis*, and other pathogens also vectored by the beetle, are responsible for about 65% of tree mortality attributed to *D. confusus* attack (Molnar 1965). Other possible roles of the fungi are as a food source for beetle larvae, conditioning of host substrate, and suppression of resistance mechanisms of the host tree (Whitney 1982).

Secondary attraction, or semiochemical mediated communication, a phenomenon which is characteristic of the Scolytidae (Borden 1982a,b), has been demonstrated for *D. confusus* (Stock and Borden 1983; Borden *et al.* 1987b). Usually a complex blend of beetle- and host-produced volatiles (Silverstein and Young 1976), i.e. pheromones and kairomones respectively (Nordlund 1981), semiochemicals are of crucial importance in determining the success of bark beetle populations in colonizing new hosts. The isolation and identification of *exo*-brevicomin as the principal aggregation pheromone, and the demonstration that *exo*-brevicomin can attract *D. confusus* to traps and induce attack on baited trees (Borden *et al.* 1987b) suggest that the beetle may be vulnerable to semiochemical-based management strategies similar to those used against other bark beetles (Borden 1989, 1990).

1.2 THESIS OBJECTIVES

The objectives of the work contained herein were:

1. to increase knowledge of the biology and impact of the western balsam bark beetle as an aid in making reliable decisions in pest management,
2 to ascertain the identity and function of putative semiochemicals used by *D. confusus*, and
3. to develop strategies and tactics for using semiochemicals in the management of *D. confusus*.

2. IMPACT OF *D. CONFUSUS* IN SUBALPINE FORESTS

2.1 INTRODUCTION

The Bulkley Timber Supply Area (TSA) was selected as a study area to assess pest damage to subalpine fir because the Annual Allowable Cut (AAC) in the TSA contains significant volumes of that species, and it was hypothesized that pest damage to subalpine fir was a major problem.

A description of the location and features of the Bulkley TSA can be found in the Bulkley Timber Supply Area Report (British Columbia Ministry of Forests (BC MoF) 1981). According to Dow (1983), "The Bulkley TSA is located in the Bulkley and Babine Valleys in the interior of the Prince Rupert Forest Region ... Productive forests are primarily mixtures of subalpine fir, lodgepole pine, and hybrid white spruce. The abundance of subalpine fir is an important floristic feature throughout the TSA, most of which is in the Sub-boreal Spruce biogeoclimatic zone."

Total Crown Forest land in the TSA is 528,000 ha, of which the net operable mature timber supply area is 39 % (204,000 ha, 49,578,000 m^3) (BCMoF 1981). Operable areas within the TSA are defined as those areas which were economically viable for sawlog timber at the time of the Bulkley Timber Supply Area Report under constraints imposed by environmental concerns, terrain, timber quality, proximity to processing facilities, and market conditions (BC MoF 1981). Subalpine fir (fir) stands account for about 41 % (20,058,800 m^3) of the total net operable volume in the TSA. Such stands, as defined by the BC MoF (1981), are those stands with > 81 % subalpine fir ("balsam types"), or stands with at least 20 % of another species, e.g. "balsam-spruce types". Pest-caused mortality of subalpine fir has been noted in the TSA since at least 1963 (Fiddick *et al.* 1964), when aerial and ground surveys were conducted, and pest activity has been reported continuously since then (Unger and Humphreys 1982a). Ground surveys to obtain volume estimates of mortality have been documented by Fiddick *et al.* (1964), and Cottrell *et al.* (1979).

The western balsam bark beetle has been the most serious pest of subalpine fir in the TSA, but other pests, particularly the eastern and the two-year spruce budworms, have also caused damage (Unger and Humphreys 1982a, 1983).

2.2 OBJECTIVES

The objectives of this study were to:

1. conduct an aerial survey of the Bulkley TSA, to establish the extent and locations of pest damage to subalpine fir, and
2. conduct ground surveys in damaged stands to verify aerial survey estimates of damage, estimate volume losses, and identify causes of subalpine fir mortality.

2.3 Methods and materials

Aerial assessment of subalpine fir mortality. I conducted word in January-March 1986. Weather conditions prevented an aerial survey of the TSA, so autumn 1985 aerial sketch mapping surveys from the BC MoF were used. I estimated the area of infestation using the average of 2 dot grid counts (Husch *et al.* 1972) (1 dot = 4.0 ha at 1:50,00 scale) and infestations were classified by forest cover type.

Where available, existing 1:10,000 scale 23 cm x 23 cm 1985 aerial colour photography taken for mountain pine beetle control programs was used instead of aerial sketch maps to determine extent and intensity of recent and current mortality based on red crowns. Red crowns are characteristic of subalpine fir from about 1 yr up to 5 yr following tree mortality such as is caused by successful western balsam bark beetle attack (Doidge 1981). Colour photos were subjectively delineated into polygons of uniform infestation density. These infestation polygons were transposed onto 1:50,000 forest cover maps, and the area estimated as for aerial sketch maps. A dot grid was used to estimate red crown coverage on photos. The base sampling unit was a square of 100 dots, representing 16 ha at a scale of 1:10,000. The number of dots touching red crowns were counted and converted to a percent of the total dots within a sampled area. The average of two randomly located sampling squares was used for estimating in polygons ≤ 200 ha, and counts from four squares were averaged for larger polygons. Polygons were then classified according to the "percentage of crown cover" showing red, as follows:

Mortality class	Percent red crown coverage
1	1 - 5
2	6 - 15
3	16 - 25
4	≥ 26

This procedure was adapted from a similar system used by Fiddick *et al.* (1964), which had 3 mortality classes (1 - 5, 6 - 30, and ≥ 30 %).. The 1964 aerial survey (Fiddick *et al.* 1964) included grey trees in the mortality classes (grey trees represented trees ≥ 4 yr after mortality, when all foliage had fallen off, but most branches and small twigs still remained). In this respect the 1964 survey was different from the 1986 photographic analysis, but was useful for comparison.

Ground survey of damage intensity. Ground plots were used to verify mortality estimates taken from colour photos. Ground plot locations were chosen to reflect the most commonly occurring combinations of mortality (% red crown coverage) and timber types (Table 2-1). Fifteen prism plots (Basal Area Factor 4[2]) were located at 100 m intervals along lines selected to give "representative coverage" through each sampled type, except for stands in mortality classes 3 and 4, which were not extensive and hence were sampled with only 10 plots per type. All trees in each plot over 18 cm diameter at 1.3 m above the root collar (= diameter at breast height, dbh) were tallied by species, dbh, mortality cause, and tree class. Tree classes were:

healthy	no obvious damage
resin	bark beetle induced resinosus on the stem - "green attack"
resin with frass	frass on the stem was considered to indicate intense, probably successful, beetle attack
red	foliage red
grey	foliage mostly absent, but fine twigs still present, and bark generally intact
snag	dead tree ≥ 3 m height, with fine twigs gone, and bark loose or absent

Statistical analysis. Data from the prism survey were used to estimate tree volumes by selecting the midpoint of height class 3 (23.95 m) to estimate height, and setting stump height and top diameter at 45 cm and 10 cm, respectively. Applying the metric volume equation[3] for interior fir ($\log_{10}$ volume = -4.291919 + 1.872930 $\log_{10}$ dbh cm + 0.998274 $\log_{10}$ height) indicated that each tallied tree represented 36.1 (± 1.8 S.E.) m^3/ha . A t-test (Zar 1984) was used to compare mean diameters of tree classes over all plots.

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[2] Basal area is the cross-sectional area, in m^2, of a tree at dbh (Society of American Foresters, Wash., D.C., 1964). The basal area factor of a prism indicates the basal area (m^2/ha) represented by each tree included in a plot.

[3] Whole stem cubic metre volume equations and tables, centimetre diameter class merchantable volume factors. Equation for interior balsam, Table 42. BC MoF Inventory Division, Victoria, B.C. 1976

Table 2-1. Allocation of sampling effort (BAF 4 prism plots) in subalpine fir stands in the Bulkley TSA, central British Columbia, by timber type and mortality class, 1986.

Timber type[a]	Mortality class	% red crown coverage	Number of plots
B, B(-), or BS			
831 p	1	≤ 5 %	45
931 p	2	6-15 %	30
831 p	2	6-15 %	30
831 m	2	6-15 %	45
831 p	3	16-25 %	10
841 g	3	16-25 %	10
831 p	4	≥ 26 %	10

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[a] See Table 2-2 for explanation of timber type symbols; (-) refers to any minor timber type as given in Table 2-2.

2.4 Results

The estimated total area of infestation based on aerial sketch mapping (Table 2-2) was approximately 17,600 ha, of which there were 2300 inoperable ha in height classes ≥ 3 (19.5-28.4 m), and 3300 were in height classes 1 and 2 (≤ 10.4 and 10.5 -19.4 m, respectively). The total operable infested area was approximately 12,000 ha.

Infestation information from the colour photographs (Table 2-2) disclosed approximately 10,000 ha of class 1 mortality, (1-5 % red crown coverage), 10,000 ha of class 2 mortality (6-15 % red crown coverage), 1700 ha of class 3 mortality (16-25 % red crown coverage), and 200 ha of class 4 mortality (≥ 26 % red crown coverage) to height class ≥ 3 stands. Approximately 5000 ha of infestations in height class ≥ 3 were inoperable. There was also approximately 2500 ha of mortality in height class 1 and 2 stands. The total operable infested area was approximately 17,000 ha.

Combining the aerial photography and sketch map surveys, subalpine fir stands in the Bulkley TSA showing various levels of mortality totalled approximately 41,900 ha in 1985-1986 (Table 2-2). Approximately 5800 ha of this total were in height class 1 and 2 in stands which are considered to be non-merchantable (BC MoF 1981), and which are not included in Table 2-2. Approximately 7300 ha of infestations in height class 3+ stands were under classification as "Environmental Protection Areas", which are considered inoperable for timber production for various reasons, including terrain sensitivity, wildlife habitat, and recreation (BC MoF 1981). There was therefore a total of 28,800 ha of operable infested area, which is approximately 10.1 % of the mature operable areas in the TSA (BC MoF 1981).

Table 2-2. Area (ha) infested by *Dryocoetes confusus* in the Bulkley TSA by timber type and mortality class, as compiled from 1:10,000 scale aerial phtographs (1985), and additional areas surveyed by aerial sketch mapping (1985).

	Hectares infested				
	Aerial photography survey				
	Mortality class				
	1	2	3	4	
Timber type[a]	1-5% area with red crowns	6-15% area with red crowns	16-25% area with red crowns	> 25% area with red crowns	Aerial sketch map survey
B 951 g					80
941 m		100			264
931 m					408
931 p	248	1120	356		1388
841 m	72	292			128
831 p	1636	1330	356	68	4324
831 m					48
832 p					12
741 g		24			
B (S) 941 m		244			
931 m	24				
931 p	156	72			104
841 g	72				
841 m	120	16	44		120
831 m	256	1332		72	716
831 p	1670	596	104		424
630 m	56				
B (Pl) 831 m	160				496
831 p	500	72			
B (Pl S) 831 p	52				
B (S Pl) 831 p		184			
731 p	56				
530 g		16			
B (S Cot) 831 p	92				
B (H) 931 p		132			12
841 m					84
831 m		32			

Table 2-2 (cont). Area (ha) infested by *Dryocoetes confusus* in the Bulkley TSA by timber type and mortality class, as compiled from 1:10,000 scale aerial photographs (1985), and additional areas surveyed by aerial sketch mapping (1985).

	Hectares infested				
	Aerial photography survey				
	Mortality class				
	1	2	3	4	
Timber type[a]	1-5% area with red crowns	6-15% area with red crowns	16-25% area with red crowns	> 25% area with red crowns	Aerial sketch map survey
B (H S) 931 m	236				
831 p	52				
B (S H) 941 m	180				
B S 941 m		56			
931 m	132	16			
931 p	136		116		196
841 m	120	228			436
831 m	552	1104	68		1372
831 p	202	718			1360
731 m		60	48		
731 p	20				104
630 m	80	64	16		
630 g	16				
530 m		8			44
B S (Pl) 931 m					172
841 m		116			
831 m	136	20			32
831 p	176	216	24		36
731 g					52
B S (Cot) 841 g	12				
B S (H) 831 m					40
B S (A) 530 m					12
B S (Pl H) 741 g					48

Table 2-2 (cont). Area (ha) infested by *Dryocoetes confusus* in the Bulkley TSA by timber type and mortality class, as compiled from 1:10,000 scale aerial photographs (1985), and additional areas surveyed by aerial sketch mapping (1985).

	Hectares infested				
	Aerial photography survey				
	Mortality class				
	1	2	3	4	
Timber type[a]	1-5% area with red crowns	6-15% area with red crowns	16-25% area with red crowns	> 25% area with red crowns	Aerial sketch map survey
B S Pl 841 g	48				36
841 m	92	20			
831 m	104	260			
831 p		28			
B Pl 831 m	56				
831 p	20	146	40		
731 m	296				
731 p	256				
B Pl S 831 m	172	80			
B Pl (S) 841 m		36			
831 m		108			12
831 p		220			156
530 m	16	188	16		
H 951 g					68
941 m					120
841 g			36		
841 m	164				20
831 m	128				
B H S 841 g	28				
B H (S) 931 m					180
831 m	12				
B H (S Pl) 831 m	56				

Table 2-2 (cont). Area (ha) infested by *Dryocoetes confusus* in the Bulkley TSA by timber type and mortality class, as compiled from 1:10,000 scale aerial photographs (1985), and additional areas surveyed by aerial sketch mapping (1985).

	Hectares infested				
	Aerial photography survey				
	Mortality class				
	1	2	3	4	
Timber type[a]	1-5% area with red crowns	6-15% area with red crowns	16-25% area with red crowns	> 25% area with red crowns	Aerial sketch map survey
B S H 841 m	60				168
S B 941 m					88
931 p					80
932 m					4
932 p					12
841 g	12	256			44
841 m					280
831 m	26				
831 p	28				
741 g		37			
640 g		16			
S B (H) 941 m					64
841 m			144		
S B H 841 g			48		
S B (Pl) 841 g					48
731 m		108			
S B Pl 831 m	92				
S B Pl(Cot) 842 g	112				
H B (S) 951 m					52
841 p	56	12			160
831			16		
H B S 931 p	80				

Table 2-2 (cont). Area (ha) infested by *Dryocoetes confusus* in the Bulkley TSA by timber type and mortality class, as compiled from 1:10,000 scale aerial photographs (1985), and additional areas surveyed by aerial sketch mapping (1985).

	Hectares infested				
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H B (Pl) 831 p	104				
H B 941 m					72
931 p					16
851 m					88
841 p					296
831 p	64				
H (B) 941 m					28
941 p					32
831 p					72
Pl B 831 m	64				20
741 g		24			
733 m	8				
731 m	12	40			
Pl B S 831 g		80			
Pl B (S) 831 g		240			
831 m		28			24
741 g	76	40			
631 m	56			3	24
Pl B Bi 430 m	24				
Pl S B 731 m	24				
Pl (S B) 831 m					20
S Pl B 831 m	28			20	

Table 2-2 (cont). Area (ha) infested by *Dryocoetes confusus* in the Bulkley TSA by timber type and mortality class, as compiled from 1:10,000 scale aerial photographs (1985), and additional areas surveyed by aerial sketch mapping (1985).

	Hectares infested				
	Aerial photography survey				
	Mortality class				
	1	2	3	4	
Timber type[a]	1-5% area with red crowns	6-15% area with red crowns	16-25% area with red crowns	> 25% area with red crowns	Aerial sketch map survey
S Pl (B) 831 m					136
S Pl B (H) 841 g	264				
630 m					12
H (S) 831 p	56				
H Pl B 530 p					32
S H (B) 951 g					20
Total	9974	10,030	1688	192	17590

[a] Letter symbols as follows: A = aspen (*Populus* spp.), B = balsam (*Abies* spp.), Cot = black cottonwood (*Populus trichocarpa* Torr. and Gray), H = hemlock (*Tsuga* spp.), Pl = lodgepole pine, S = spruce (*Picea* spp.),. Minor species comprising 10-19 % of gross volume are bracketed. First number refers to age class (yr): 4 = 61-80, 5 = 81-100, 6 = 101-120, 7 = 121-140, 8 = 141-250, 9 = 251+. Second number refers to height class (m): 1 = 0-10.4, 2 = 10.5-19.4, 3 = 19.5-28.4, 4 = 28.4-37.4. Third number refers to stocking class: 0 = all immature, 1 = all mature, 76+ trees/ha of 27.5+ cm dbh, 2 = all mature, 0-75/ha, 27.5cm dbh. Letters on right refer to site index: g = good, m = medium, p = poor.

Most mortality (89.5 % of the infested area) was in fir types, on poor or medium sites, in stands ≥ 141 yr (age classes 8 and 9). This trend reflects the situation in the Bulkley TSA, where most sites (87 % by area) are poor or medium, and most of the fir types are in age classes 8 and 9 (BC MoF 1981). It would be desirable to sample a wider variety of types before commenting on mortality in age classes 5, 6, and 7.

Mortality within stands was generally distributed in a discontinuous "clumped" pattern, that is, red trees usually occurred in groups of 2 or more. These groups often occurred throughout entire stands, sometimes encompassing > 500 ha. This pattern appears to be typical of the western balsam bark beetle, and detailed mapping of this type of mortality from an aircraft is difficult (pers. obsv.).

The primary agent of damage noted in ground surveys was the western balsam bark beetle. *D. confusus* may act in much the same manner as the spruce beetle, preferentially utilizing windfall and cut-block edge blowdown, yet able to kill apparently healthy trees. No major defoliation was noted. Winter conditions made it impossible to sample for root diseases such as *Inonotus* (*Polyporus*) *tomentosus* (Fr). Gilbn. or *Armillaria* (Vahl.: Fr. Quel) spp., although mortality does occur (Unger and Humphreys 1982a). A survey conducted by the Canadian Forestry Service Forest Insect and Disease Survey indicated that a mean of 20 % of trees in surveyed stands were infected with the heart rots *Phellinus* (= *Fomes*) *pini* (Thore:Fr) Pilat or *Echinodontium tinctorium* (Ell. and Ev.) Ell. and Ev. (Unger and Humphreys 1982b).

The mean total volume in ground-surveyed stands was 312 m^3/ha, 87 % (271 m^3/ha) of which was subalpine fir. Dead trees accounted for an average of 38 % (118 m^3/ha) of the total volume for all tree classes in all stands (Table 2-3). Snags accounted for most (mean 60 %) of total dead volume (Table 2-3). These stems were often so deteriorated that identification of mortality agents was not possible.

Table 2-3. Volume and diameter data from BAF 4 prism surveys of subalpine fir mortality in the Bulkley TSA, central British Columbia, 1986.

Criterion assessed[a]	Timber type and location			
	B(S) 831 p Gramaphone Ck.	B 831 p Harold Price Ck.	B(S) 831 p Tenas Ck.	B 931 p Telkwa microwave
Mortality class	1	1	1	2
Stand dbh (cm) (Mean ± SE)	32	36	40	38
Total volume (m^3/ha)	231	260	460	229
Subalpine fir volume (%)	87	79	95	92
H dbh (cm) (Mean ± SE)	32 ± 1.2	33 ± 1.4	41 ± 1.1	34 ± 1.3
H volume (m^3/ha)	165	173	262	142
Red dbh (cm) (Mean ± SE)	--	--	42 ± 2.5	43 ± 6.2
Red volume (m^3/ha)	--	--	24	14
Gy dbh (cm) (Mean ± SE)	--	42	42 ± 2.6	45
Gy volume (m^3/ha)	--	7	14	5
Sn dbh (cm) (Mean ± SE)	32 ± 2.0	32	39 ± 1.0	35 ± 1.72
Sn volume (m^3/ha)	60	55	130	53
R,Rf dbh (cm) (Mean ± SE)	28	35 ± 2.0	36 ± 2.9	34 ± 3.7
R,Rf volume (m^3/ha)[b]	5	24	19	14
Total mortality (m^3/ha)	65	86	187	86

Table 2-3 (cont.). Volume and diameter data from BAF 4 prism surveys of subalpine fir mortality in the Bulkley TSA, central British Columbia, 1986.[a]

	Timber type and location			
Criterion assessed[a]	B(S) 831 p Gramaphone Ck.	B 831 p Harold Price Ck.	B(S) 831 p Tenas Ck.	B 931 p Telkwa microwave
Mortality class	2	2	2	2
Stand dbh (cm) (Mean ± SE)	34	38	38	44
Total volume (m^3/ha)	274	286	231	351
Subapline fir volume (%)	88	100	89	81
H dbh (cm) (Mean ± SE)	32 ± 1.2	34 ± 1.2	36 ± 1.4	36 ± 1.2
H volume (m^3/ha)	168	140	195	226
Red dbh (cm) (Mean ± SE)	34	49 ± 4.2	36 ± 4.9	60
Red volume (m^3/ha)	7	24	10	2
Gy dbh (cm) (Mean ± SE)	38 ± 3.1	40	46	56
Gy volume (m^3/ha)	14	10	6	7
Sn dbh (cm) (Mean ± SE)	31 ± 1.4	36 ± 1.5	40 ± 1.9	36 ± 1.1
Sn volume (m^3/ha)	58	72	82	94
R,Rf dbh (cm) (Mean ± SE)	36 ± 2.0	33 ± 2.4	33 ± 3.0	34 ± 1.5
R,Rf volume (m^3/ha)[b]	26	41	16	22
Total mortality (m^3/ha)	105	147	114	125

Table 2-3 (cont.). Volume and diameter data from BAF 4 prism surveys of subalpine fir mortality in the Bulkley TSA, central British Columbia, 1986.[a]

	Timber type and location			
Criterion assessed[a]	B(S) 831 p Gramaphone Ck.	B 831 p Harold Price Ck.	B(S) 831 p Tenas Ck.	B 931 p Telkwa microwave
Mortality class	2	2	3	3
Stand dbh (cm) (Mean ± SE)	36	47	46	45
Total volume (m^3/ha)	371	435	284	289
Subapline fir volume (%)	51	91	95	91
H dbh (cm) (Mean ± SE)	35 ± 1.2	48 ± 1.6	43 ± 1.7	44 ± 1.6
H volume (m^3/ha)	264	260	180	202
Red dbh (cm) (Mean ± SE)	40 ± 4.1	44	59 ± 4.1	41 ± 3.3
Red volume (m^3/ha)	12	29	14	2
Gy dbh (cm) (Mean ± SE)	37	54	51 ± 3.1	58
Gy volume (m^3/ha)	19	10	17	7
Sn dbh (cm) (Mean ± SE)	35 ± 2.3	46 ± 2.1	45 ± 2.5	46 ± 2.8
Sn volume (m^3/ha)	51	108	48	60
R,Rf dbh (cm) (Mean ± SE)	35 ± 1.6	45 ± 3.5	34 ± 3.5	37 ± 4.2
R,Rf volume (m^3/ha)[b]	24	29	17	12
Total mortality (m^3/ha)	106	176	96	81

Table 2-3 (cont.). Volume and diameter data from BAF 4 prism surveys of subalpine fir mortality in the Bulkley TSA, central British Columbia, 1986.[a]

	Summary Data			
Criterion assessed[a]	B(S) 831 p Gramaphone Ck.	B 831 p Harold Price Ck.	B(S) 831 p Tenas Ck.	B 931 p Telkwa microwave
Mortality class	4	--	--	--
Stand dbh (cm) (Mean ± SE)	37	36	39	39
Total volume (m^3/ha)	356	317	311	312
Subapline fir volume (%)	34	86	85	87
H dbh (cm) (Mean ± SE)	38 ± 1.3	35	36	37
H volume (m^3/ha)	185	200	199	198
Red dbh (cm) (Mean ± SE)	35 ± 2.1	42	44	44
Red volume (m^3/ha)	26	8	14	13
Gy dbh (cm) (Mean ± SE)	36 ± 1.9	42	45	45
Gy volume (m^3/ha)	41	7	10	12
Sn dbh (cm) (Mean ± SE)	37 ± 2.8	34	37	38
Sn volume (m^3/ha)	51	82	74	71
R,Rf dbh (cm) (Mean ± SE)	38 ± 1.9	33	36	35
R,Rf volume (m^3/ha)[b]	43	16	25	22
Total mortality (m^3/ha)	161	113	123	118

[a] Symbols used in row headings are as follows: Red = red crown, Gy = gray, Sn = snag, R,Rf = green attack, H = healthy. S.E. not calculated for < 5 trees.

[b] Data from resin (R) and resin + frass (Rf) tree classes combined because of small sample size.

Stands with 1 - 5 % red crown coverage on photos (mortality class 1) had a mean of 8 m^3/ha of red attack, and 16 m^3/ha in R,Rf (green attack) trees. This is similar to estimates by Fiddick *et al.* (1964) of 9 m^3/ha mortality in stands with 1 - 5 % damage, excluding green attack because there was (and is) no satisfactory method of determining which trees will survive new attack. Stands with 6 - 15 % red crown coverage had higher levels of damage (14 ^{3}/ha red, 25 ^{3}/ha R,Rf) (Table 2-3). The mean dbh of older beetle attacked trees (red = 44 cm, gray = 45 cm) was larger than average stand diameters (39 cm, t-test, $p \leq 0.10$). Diameters of "green attack" (R,Rf, mean = 35 cm) trees were generally the same as or smaller than stand average diameters (Table 2-3).

Mortality volumes in heavily damaged stands (≥ 16 % damage, excluding green attack) were 83 m^3/ha and 96 m^3/ha for the 1964 and 1986 surveys respectively. Green attack for 1986 was estimated to be 22 m^3/ha. Assuming that all R,Rf trees survive, red trees retain foliage for 5 years (Doidge 1981), and that gray trees represent a 1 year transition stage between red and snag trees, total mortality for 6 years prior to and including 1985 can be estimated by adding gray and red volumes (mean for all blocks) from Table 2-3 as being 25 m^3/ha. This estimate represents 4.2 m^3/ha of annual mortality.

2.5 Discussion

Past estimates of western balsam bark beetle infestations in the Pr. Rupert Region have varied widely. It was reported by the Canadian Forestry Service in 1963 that "almost every stand in the region has been affected to some extent" (Unger and Humphreys 1982a). Estimates since 1980 for the Pr. Rupert Forest Region have been 2,450 ha (Unger and Humphreys 1982b), and 8,600 ha (Unger and Humphreys 1983). An estimate for the Bulkley TSA was 18,000 ha (Unger and Humphreys 1985), inexplicably greater than the entire Prince Rupert Region. The estimate for the Bulkley TSA in 1985 was 34,300 ha, based on aerial sketch mapping by the BC MoF (Unger and

Stewart 1986). Much of the variation in reported estimates is due to the fact that surveys are seldom comprehensive or complete (Unger and Stewart 1986). This was the case for the 1985 aerial survey (K. Bush, pers. comm.[4]), which means that the estimates in Table 2-2 are conservative.

The Bulkley TSA AAC calculation allows for an annual mortality due to insects and diseases of 42,500 m^3 in subalpine fir types in a sawlog economy (BC MoF 1981). This equals 1.5 m^3/ha over a 28,000 ha pest infestation. My estimate of4.2 m^3/ha is very close to the estimate of 4.4 m^3/ha made by Unger and Stewart (1986), who surveyed trees with foliage turning from green to red. Both of these estimates appear to exceed the annual allowance of 1.5 m^3/ha. However, the BC MoF (1981) assumes 50 % salvage of these stands, which, if realistic, cuts down estimated loss to approximately 2.1 m^3/ha, which still exceeds the annual allowance by at least 25 %. Further, the subalpine fir types within the Bulkley TSA are assumed to have a merchantable volume that is only 50 % of gross volume (BC MoF 1981), leaving an estimated annual loss of 1 m^3/ha, which is within the range of allowable loss. Such a large allowance for decay and/or loss would seem to negate the effects of pest damage in individual stands. It is important to note, however, that recent mortality (red and grey trees) observed in this study was concentrated on the largest trees, which will adversely affect stand merchantability. Prism plot data indicate that larger stems in the ground surveyed stands were already dead. Molnar (1965) suggested that small (young?) trees seemed more resistant to balsam bark beetle attack. The preference of attacking beetles for larger trees is typical of other important scolytids (Safranyik *et al.* 1974, Schmid and Frye 1977).

More recently, in subalpine forests in the adjacent Morice TSA, accumulated volume loss has exceeded 30 % of stand volume (Garbutt and Stewart 1991).

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4. Bulkley Forest District, BC MoF, Smithers, B.C.

On the basis of my results I recommend that an aerial survey be conducted to obtain comprehensive and complete information on subalpine fir mortality in the Bulkley TSA and in other areas of the province with significant subalpine fir volumes. The BC Ministry of Forests should carefully re-evaluate volume expectations in over mature subalpine fir stands. Indications are that allowances for losses due to insects and diseases may have to be increased, and that residual stands are reduced in merchantability. The rate at which stands become non-merchantable should be determined.

There is a clear need for a comprehensive study to relate pest damage to volume loss. Tree mortality does not necessarily mean volume loss, but there is a limit on the length of time a dead tree remains useful. Considering the conservative nature of the mortality estimates herein, present assumptions of 50 % salvage may not be realistic. "Grey" trees and "old reds" are marginally useful for saw logs (Dobie and Wright 1978; pers. obsv.). In fact, large areas of these forests may be in a salvage-only situation, requiring special processing procedures, and returning only minimum stumpage to the Crown, e.g. McKendrick Pass in the Bulkley TSA, and areas in the adjacent Morice TSA (Garbutt and Stewart 1991). Any stand in age class ≥ 8 is obviously at risk. Susceptibility of younger stands (age classes 5 - 7) should be carefully assessed. Regardless of the outcome of the recommended comprehensive study there are sufficient data on hand to justify implementation of cost-effective pest management strategies and tactics to reduce tree mortality.

3. SEMIOCHEMICAL-BASED COMMUNICATION IN *DRYOCOETES CONFUSUS*

3.1 INTRODUCTION

3.1.1 **Semiochemical-based communication in the Scolytidae**

For insects, odours are important in the selection of suitable hosts/sites for feeding, egg laying, mate selection, courtship, resource allocation, and other behaviours (Birch 1982). The "message bearing chemicals" which carry this information, and which, in a natural context, elicit behavioural and/or physiological responses, are called semiochemicals (Nordlund 1981). Following the terminology of Nordlund (1981), semiochemicals can be of four major types. Semiochemicals that mediate intraspecific communication are called pheromones (Shorey 1973). A second group of semiochemicals, allelochemics, carry interspecific messages. These are termed allomones if an adaptive benefit accrues to the emitting organism, or kairomones if the perceiving organism benefits (Nordlund 1981). Synomones evoke responses that are adaptively favourable to both the emitter and the receiver (Nordlund 1981).

History has validated the hypothesis by Wood *et al.* (1966) that pheromones inducing concentration and mass-attack on trees are characteristic of the Scolytidae. Major reviews of insect chemical communication include significant reference to the Scolytidae (Shorey 1973; Borden 1977; Brand *et al.* 1979; Bell and Cardé 1984; Lewis 1984; Payne *et al.* 1986; Prestwich and Blomquist 1987; Ridgway *et al.* 1990). In addition, the prominence given to the topic of semiochemicals in reviews of the Scolytidae (or in forest entomology reviews generally) is indicative of the great significance of semiochemicals in studies of biology, ecology, population dynamics, genetics and management (Rudinsky 1962; Berryman *et al* 1978; Mitton and Sturgeon 1982; Thatcher *et al.* 1980; Berryman 1988; Payne *et al.* 1988).

There have been several recent reviews of the role of semiochemicals in the life history of the Scolytidae (Wood 1982; Borden 1982a, 1984, 1985; Birch 1984; Byers 1989). Most divide the life history of emerging new adult beetles into 3 or 4 distinct or variously combined phases; dispersal (migration), new host selection, concentration, and establishment.

Some newly-emerged dispersing (flying) beetles may not show any response to semiochemicals, but certain physiological changes, including metabolism of lipid reserves, result in a behavioural change allowing the possibility of a positive response (Borden *et al.* 1986; Anderbrandt and Schlyter 1989). This requisite period of activity appears to be a mechanism for ensuring "long-range dispersal" and hence discovery of distant food sources (Atkins 1966; Ricklefs 1979), temporary escape from natural enemies (Ricklefs 1979), and outbreeding (Borden 1982a). For some of the earliest-emerging "pioneer" beetles, long range dispersal may also be a function of the local absence of pheromones (Wood 1982). Alternatively, emerging beetles with little lipid reserve may show an immediate response to attractants and disperse over lesser distances, thereby minimizing energy expenditure and exposure to predators (Wood 1982), and fully utilizing locally available resources. It is probable that a continuum of the two conditions exists for most species (Wood 1982). Hunt and Borden (1989) hypothesize that a reduction in lipid reserves may also be a prerequisite for maximum pheromone production in adult beetles.

Selection of new hosts involves elements of *primary attraction*, a directed process (Wood 1982) in which beetles orient preferentially, and over "long range", to host tree species and/or stressed host trees in response to kairomones emanating from the trees, (Rudinsky 1966; Moeck 1981; Borden 1982a,b; Wood 1982), and *random search*, in which beetles land on potential host trees selected randomly and/or with some visual cues (Moeck 1981; Wood 1982). In random search, host suitability is tested at close range, sometimes with direct sampling by boring through the bark into the phloem (Birch 1983).

Evidence exists for both modes of host selection, and Borden (1982a) concluded that "interspecific differences preclude sweeping generalization." More recently, Gries *et al.* (1989) demonstrated by computer simulation that reliance soley on random searching would be insufficient to sustain a population of the European spruce bark beetle at a constant level.

? Selection of a suitable host initiates the process of *secondary attraction* (Birch 1983), wherein a complex of beetle-produced chemicals (pheromones) and host volatiles (kairomones) are produced as a consequence of beetle attack (Borden 1982a); it is apparent that pheromones and allelochemics usually act as multi-component blends (Silverstein and Young 1976). A given semiochemical produced by a bark beetle may have more than one function, depending on the context in which it is perceived, or on the dosage (rate of production or release into the environment) (Nordlund 1981). Semiochemicals in the Scolytidae serve three primary functions: induction of mass aggregation of conspecifics of both sexes on a host, regulation/termination of aggregation to optimise resource allocation on the initial host, ultimately causing switching of attack to another nearby host, and mediation of inter-specific communication (Borden 1982a), i.e., induction or inhibition of aggregation of species that compete for the same resource, and mediation of host-finding by commensal and entomophagous insects (Borden 1989).

Most bark beetle pheromones are secondary alcohols apparently derived from metabolism of host resin monoterpenes, or bicylic ketals of less well understood biosynthetic origin (Hughes 1973, 1974; Vanderwel and Oehlschlager 1987). Microorganisms associated with bark beetles have been implicated in production of aggregation pheromones (Vanderwel and Oehlschlager 1987), but appear to be of potentially greater importance in the production of antiaggregation pheromones (Luefvén *et al.* 1984; Birgersson and Birgstrom 1989; Hunt and Borden 1989).

Specific activity of structural and optical chemical isomers, alone, or in some defined ratio of combination with their antipodes, is now known to be common in insect chemical communication (Mori 1984; Silverstein 1988). When a single enantiomer is produced, the other enantiomer is usually less active or benign, and occasionally inhibitory (Silverstein 1988). Rarely does the unproduced antipode have an effect that is additive or synergistic to the naturally produced enantiomer (Silverstein 1988), although there is a suggestion that this occurs in the mountain pine beetle and *D. confusus*. Borden *et al.* (1987a) showed that the response of mountain pine beetles to traps baited with myrcene, *trans*-verbenol, and *exo*-brevicomin suggested an additive effect when the (+) and (-) enantiomers of *exo*-brevicomin were combined, despite the fact that male *D. ponderosae* produce > 98 % (+)-*exo*-brevicomin (Schurig *et al.* 1983). Similarly, in a bioassay of walking female *D. confusus* Borden *et al.* (1987b) found no difference in response to large amounts (more than 50 ng) of (±)-, (+)-, or (-)-*exo*-brevicomin. They attributed response to (-)-*exo*-brevicomin to the presence of small amounts of the (+) enantiomer. At the lowest dose (5 ng), however, response by females was significantly greater to (±)-*exo*-brevicomin than to either enantiomer, and was in fact the highest response of all treatments, even though male *D. confusus* produce > 99 % (+)-*exo*-brevicomin (Schurig *et al.* 1983).

Inter- and intra-population variation in quantity and quality of pheromone blends appears to be common in scolytidae (Lanier 1972; Birgersson *et al.* 1984; Slessor *et al.* 1985; Borden *et al.* 1986; Hunt *et al.* 1986; Birgersson *et al.* 1988; Miller *et al.* 1989). Sources of variation include geographic location, environmental factors influencing beetle vigour, host quality, levels of precursors in host tissues, and rates and composition of resin produced by hosts in response to beetle attack (Leufven and Birgersson 1987; Birgersson *et al.* 1984; Birgersson *et al.* 1988; Berisford *et al.* 1989; Gries *et al.* 1990). Temporal variation in the quantity of pheromone produced may result from differential ingestion and defecation rates (Birgersson *et al.* 1984). Miller *et al.* (1989) suggest that geographic variation in the specificity and separation of pheromone "communication channels" (Cardé and Baker 1984) should occur in response to differences in competition for channels. Finally, Miller *et al.* (1989) hypothesize that variation in pheromone-producing enzyme systems, which may lead to variations in pheromone chirality, is a quantitative genetic trait for individual beetles. Development of "resistance" to pheromone blends, especially where mass trapping is employed, is a possible consequence of this plasticity within the semiochemical communication system of scolytids (Lanier 1972; Borden *et al.* 1986; Haynes and Baker 1988; Miller *et al.* 1989)

3.1.2 Semiochemical-based communication in *Dryocoetes* spp.

Empirical evidence for attraction of *Dryocoetes affaber* (Mannerheim) and *Dryocoetes autographus* (Ratzeburg) to semiochemicals (*trans*-verbenol, verbenol, suedenol, and/or frontalin) and/or to uninfested, freshly-felled spruce logs was noted by Furniss *et al.* (1976). The first experimental evidence for secondary attraction in the genus *Dryocoetes* was found by Nilssen (1979), who demonstrated that male and female *D. hectographus* Reitter and *D. autographus* were attracted to frass from males of their own species. Subsequently, it was found that polygamous male *D. confusus* produced a semiochemical-based secondary attraction when attacking new hosts (Stock and Borden 1983). Schurig *et al.* (1983) disclosed that abdominal extracts of male *D. confusus* excised from subalpine fir logs after 24 h contained *exo*- and *endo*-brevicomin in approximately an 18:1 ratio, that *exo*-brevicomin was present as 99.2 % (+) enantiomer, and that *endo*-brevicomin was 81.6 % (+) enantiomer. Borden *et al* (1987b) also found verbenone, myrtenol, *trans*-pinocarveol, *cis*- and *trans*-*p*-menthen-7-ol, 3-caren-10-ol, and other monoterpenes and sesquiterpenes in male abdominal extracts. In addition, emergent, fed, or fed and mated males contained *trans*-verbenol, whereas only feeding females, or females allowed to join males, contained *trans*-verbenol (Borden *et al* 1987b).

(+)-*exo*-Brevicomin is attractive to female *D. confusus* in laboratory bioassays but because the (-) enantiomer is apparently benign, (+)- or (±)-*exo*-brevicomin can be used to induce beetles to attack standing trees (Borden *et al.* 1987b). Field tests showed that (±)-myrtenol was important as a synergist with *exo*-brevicomin for increasing beetle catch in multiple-funnel traps, but was not attractive by itself (Borden *et al.* 1987b).

Male *D. autographus* also produce an attractive mixture of *exo*- and *endo*-brevicomin (Kohnle and Vité 1984). (+)-*endo*-Brevicomin is attractive to female *D. autographus*, while the antipode is inactive (Kohnle 1985), but the role of *exo*-brevicomin has not been clarified.

endo-Brevicomin has been reported as an antiaggregation pheromone in the southern pine beetle and the mountain beetle (Borden 1985). It is repellent to the southern pine beetle at high release rates (Payne 1981), but the (+) enantiomer was shown to be an attractive pheromone, while the (-) enantiomer was found to be repellent (Vité *et al.* 1985). The western pine beetle produces both *exo*- and *endo*-brevicomin; the former is an aggregation pheromone, while no role has been discovered for the latter (Wood *et al.* 1976; Bedard *et al.* 1980).

3.1.3 **Objectives**

My objectives were to:

1. determine the response of *D. confusus* to the enantiomers of *exo*-brevicomin in the field,
2. test the effect of varying release rates of *exo*-brevicomin on aggregation of *D. confusus* to baited trees, and
3. test the hypothesis that *endo*-brevicomin is also a pheromone for *D. confusus*.

3.2 ACTIVITY OF KNOWN AND PUTATIVE SEMIOCHEMICALS

3.2.1 ***exo*-Brevicomin**

3.2.1.1 Materials and methods

Enantiomers of *exo*-brevicomin were available from a previous study (Johnson and Oehlschlager 1982): (+)-*exo*-brevicomin, 86 % optical purity, and (-)-*exo*-brevicomin, 90 % purity. Racemic *exo*-Brevicomin (99.7% chemical purity, Albany Intl. Co., Columbus Ohio (Conn *et al.* 1983) or its enantiomers were released from glass capillary tubes (releasing 0.2 mg/24 h/tube, as determined for 20° C in the laboratory).

In a 10-replicate randomized complete block experiment from 21 July - 13 August, 1986 at Walcott Creek, B.C., 8-unit multiple funnel traps (Lindgren 1983) spaced 50 m apart were unbaited, or baited with (±)-, (+)-, or (-)-*exo*-brevicomin. This experiment was repeated 23 June - 3 July, 1987 at Willow Lake, B.C., with 5 replicates, and one additional treatment in which individual capillary tubes containing (+)-, or (-)-*exo*-brevicomin were combined in one bait as a comparison against (±)-*exo*-brevicomin. In a third 10-replicate randomized complete block experiment in 1986 at Gramaphone Creek, B.C., the glass tubes containing *exo*-brevicomin were mounted in cardboard holders (PheroTech Inc., Delta, B.C.), and affixed prior to beetle flight as high as possible on the north side of selected apparently healthy trees ≥ 20 cm diameter at 1.3 m ht (dbh), with a 50 m inter-tree spacing. After beetle flight trees were classified as attacked (with resin flow as visible evidence of beetle activity), mass attacked (with frass on the bole as evidence of successful beetle attack), or unattacked. Attack on trees was quantified by counting attack holes on a 30 x 30 cm sample of bark peeled from the west side of trees at dbh.

The effect of varying release rates of *exo*-brevicomin was field tested in a 10-replicate randomized complete block experiment in 1986 at Fulton River, B.C. Cardboard holders containing 1, 5, and 10 glass capillary tubes, collectively releasing (±)-*exo*-brevicomin at 0.2, 1.0, and 2.0 mg/24 h respectively, were affixed to trees spaced at 50 m as described above. In a second 10-replicate experiment in 1986 at Willow Lake, B.C., holders with 1, 2, 3, 4, and 5 glass capillary tubes collectively releasing (±)-*exo*-brevicomin at 0.2, 0.4, 0.6, 0.8, and 1.0 mg/24 h respectively, were affixed to trees spaced at 50 m. A third randomized complete block experiment in 1986 at McKendrick Pass, B.C., assessed the effect of baiting 1, 3, or 5 trees in spots spaced 50 m apart. Each selected tree was baited with (±)-*exo*-brevicomin released at 0.4 mg/24 h, so the maximum total release rate in a spot was 2.0 mg/24 h. In the latter two experiments, two survey strips 30 m long and 10 m wide were run in opposite directions starting from baited trees, or the geographic centre of a "spot". All subalpine fir trees ≥ 20 cm dbh within each strip were classified as healthy, red, grey, attacked, or mass attacked. Dbh, and distance from the origin of each strip were recorded for each tree.

Data from all experiments were analyzed using an analysis of variance and Student-Newman-Keuls test (Number Cruncher Statistical System 1988). Data from the experiment testing for enantiomeric activity of *exo*-brevicomin on trees were first transformed using the square root of $(x + 3/8)$, and the actual mean number of attacks per m^2 are reported with the back-transformed upper 95% confidence limit (Sokal and Rohlf 1981).

3.2.1.2 Results

In 1986 (±)-*exo*-brevicomin was more attractive in traps than either (+)- or (-)-*exo*-brevicomin, which did not attract significantly more beetles than the unbaited control traps (Table 3.2-1). In 1987, traps baited with (±)- or (+)-*exo*-brevicomin attracted more beetles than unbaited traps or those baited with (-)-*exo*-brevicomin. (+)-*exo*-Brevicomin was also superior to the treatments with separate enantiomers released from the same holders, which attracted fewer beetles than (+)-*exo*-brevicomin, but more than

Table 3.2.1-1. Catch of *D. confusus* in multiple funnel traps baited with enatiomers of *exo*-brevicomin, Walcott Ck., B.C., 1986, and Willow Lake, B.C., 1987.

Year	Bait treatment	Number of replicates	Release rates (mg/24 h)	Number of beetles per trap[a] (mean ± S.E.)
1986	(±)-*exo*-brevicomin	10	0.4	25.7 ± 10.51a
	(+)-*exo*-brevicomin	9	0.2	2.6 ± 1.02b
	(-)-*exo*-brevicomin	9	0.2	3.1 ± 1.11b
	blank control	9	-	0.2 ± 0.22b
1987	(±)-*exo*-brevicomin	4	0.8	25.0 ± 6.02a
	(+)- and (-)-*exo*-brevicomin	5	0.4 + 0.4	7.4 ± 2.60b
	(+)-*exo*-brevicomin	5	0.4	13.8 ± 3.43a
	(-)-*exo*-brevicomin	5	0.4	2.0 ± 1.30c
	blank control	5	-	0.6 ± 0.40c

[a] No significant difference between sexes in 1986 or 1987, Newman-Keuls test, $p \leq 0.05$. Means within columns for either experiment followed by the same letter are not significantly different, Newman-Keuls test, $p \leq 0.05$.

Table 3.2.1-2. Attack by *D. confusus* on *A. lasiocarpa* baited with enantiomers of *exo*-brevicomin, Gramaphone Ck, B.C., 1986.

Bait	Number of replicates	Release rates (mg/24 h)	No. of attacks per m^2 on mass attacked trees (Mean with upper 95% conf. limit)[a]	Percent of trees mass attacked
(±)-*exo*-brevicomin	9	0.4	48.9 (80.11)a	78
(+)-*exo*-brevicomin	10	0.2	21.1 (34.60)ab	50
(-)-*exo*-brevicomin	10	0.2	20.0 (34.60)ab	30
blank control	11	-	0.0b	0

[a] Means within columns followed by the same letter are not significantly different, Newman-Keuls test, $p \leq 0.05$.

(-)-*exo*-brevicomin. (±)-*exo*-Brevicomin induced mass attack on 78 % of baited trees at an attack density of 48.9 per m^2, significantly more than on unbaited control trees, while(+)- and (-)-*exo*-brevicomin induced intermediate attack frequency and density (Table 3.2.1-3).

(±)-*exo*-Brevicomin released at 0.2 mg/24 h induced few trees to be mass attacked (Table 3.2.1-3). Most trees baited with (±)-*exo*-brevicomin released at 1.0 or 2.0 mg/24 h release rates were mass attacked. Attack densities were significantly higher than on unbaited control trees only at the release rates of $\geq$ 0.6 mg/24 h (Table 3.2.1-3). There were no significant differences in numbers of available trees (unattacked prior to treatment, $\geq$ 20 cm at dbh) per 10 m radius (ANOVA, 12.3 ± 0.74 trees, $p = 0.2814$ in 1985, and 5.8 ± 0.39 trees, $p = 0.5426$ in 1986). Significantly more trees were attacked within a 10 m radius of trees baited with (±)-*exo*-brevicomin released at 2.0 mg/24 h than at the 2 lower release rates in 1985 (Table 3.2.1-3).

A release rate of 0.8 mg per 24 h was found to be as good as or better than other treatments in terms of the numbers of baited trees mass attacked, attack density, and the number of trees attacked within 10 m of baited trees in 1986 (Table 3.2.1-4). Results from the 30 m strip survey indicated that attack on surrounding trees is concentrated within 10 m of baited trees. There was no significant difference between treatments in the number of attacked trees beyond 10 m of the treatment centres (ANOVA, $p \leq 0.01$).

Combining a high release rate with baiting more than one tree in a spot resulted in an intensification of attack on baited trees, and significant increases in the number of attacked trees within 10 m of the center of each spot (Table 3.2-4). Results of the 30 m strip survey again indicated that attack was concentrated within 10 m of the treatment centres, and there was no significant difference between treatments in the number of attacked trees beyond 10 m of the treatment centres (ANOVA, $p \leq 0.01$).

Table 3.2.1-3. Effect of varying release rate of (±)- *exo*-brevicomin on attack by *D. confusus* on *A. lasiocarpa*, Fulton River, B.C., 1985 and Willow Lake, B.C., 1986.

Year	Release rate of *exo*-brevicomin (mg/day)	Number of replicates	Percent of baited trees mass attacked	No. attacks per m^2 on newly attacked trees (Mean ± S.E.)[a]	No. of all newly attacked trees within 10 m of baited trees (Mean ± S.E.)[a]
1985	2.0	10	90.0	70.0 ± 17.14a	2.9 ± 0.72a
	1.0	10	80.0	75.6 ± 24.56a	1.3 ± 0.50b
	0.2	9	11.1	16.7 ± 13.38b	0.5 ± 0.31b
	blank control	11	0.0	0.0b	0.3 ± 0.21b
1986	1.0	10	80.0	75.6 ± 30.44ab	2.0 ± 0.44a
	0.8	10	80.0	165.6 ± 34.24a	2.5 ± 0.55a
	0.6	9	55.0	77.8 ± 32.61ab	1.3 ± 0.33ab
	0.40	11	36.0	48.5 ± 21.04b	1.5 ± 0.39ab
	0.2	10	20.0	1.1 ± 1.11b	1.1 ± 0.38ab
	blank control	10	0.0	0.0b	0.3 ± 0.15b

[a] Means within columns followed by the same letter are not significantly different, Newman-Keuls test, $p \leq 0.05$.

Table 3.2.1-4. Effect of multiple-tree baiting with (±)-*exo*-brevicomin released at 0.4 mg/24 h, on attack by *D. confusus* on *A. lasiocarpa*, McKendrick Pass, B.C., 1986. N = 10.

Treatment	Percent of baited trees mass attacked	No. of newly-attacked trees within 10 m of baited trees (Mean ± S.E.)[a]
5 trees baited	40.3	5.9 ± 0.41a
3 trees baited	14.3	3.8 ± 0.36b
1 tree baited	4.7	1.5 ± 0.22c
blank control	0.0	0.3 ± 0.15d

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[a] Means followed by the same letter are not significantly different, Newman-Keuls test, $p \leq 0.05$. No significant difference between treatments in number of available trees (7.2 ± 0.39, including baited trees) per 10 m radius, ANOVA, $p = 0.5152$.

3.2.1.3 Discussion

Results of these field experiments indicate that (±)-*exo*-brevicomin is more attractive to *D. confusus* than either enantiomer alone, suggesting that the preferential response to racemic pheromone observed in laboratory bioassays by Borden *et al.* (1987b) may not have been an artifact, and emphasizing the importance of pheromone biology and dose-response studies (Vité *et al.* 1985; Tumlinson 1988; Miller 1990). These results together with those of Borden *et al.* (1987a, b) for *D. confusus* and mountain pine beetle, respectively, represent apparently unusual cases (Silverstein 1988) because they imply a synergistic and/or additive effect when a naturally produced enantiomer is combined with an antipode that is not produced. The results further suggest that, for *D. confusus*, laboratory bioassay doses of > 5 ng, as used by Borden *et al* (1987b), may be so large that they obscure subtle aspects of beetle behaviour in bioassays (Tumlinson 1988; Dickens *et al* 1985).

Southern pine beetles (Payne *et al.* 1982), some populations of pine engraver (Lanier 1972; Lanier *et al.* 1980; Miller *et al.* 1989), the ambrosia beetle *Gnathotricus sulcatus* (Borden *et al.* 1976, 1980), the flour mill grain beetle (Millar *et al.* 1985), and honey bees (Slessor *et al.* 1988) all produce and respond optimally to chiral mixtures of the enantiomers of certain pheromone mixtures, demonstrating synergism between enantiomers. The southern pine beetle responds equally well to (±)-frontalin and the single enantiomer, (-)-frontalin, that is produced in relatively greater quantities than the antipode (Payne *et al.* 1982). Pine engravers in eastern North America (Lanier *et al.* 1980) and *G. sulcatus* (Borden *et al.* 1976) respond relatively poorly to the individual enantiomers.

Ips spp., *G. sulcatus*, and *D. confusus* may tolerate some variation in pheromone component blends. For example, most pine engravers from the Kootenay region of British Columbia contained almost pure (*R*)-(-)-ipsdienol, but some beetles contained appreciable amounts of (*S*)-(+)-ipsdienol, a pattern similar to that found in beetles in California (Miller *et al.* 1989). When pine engravers in California are confronted with a mixture of enantiomers response is inhibited (Birch *et al.* 1980), while response by pine engravers in New York to similar stimuli is enhanced (Lanier *et al.* 1980), yet intra-population variation occurs for both these groups of beetles (Miller *et al.* 1989). These results, in light of Borden *et al.* (1976, 1980, 1987b) and Schurig *et al.* (1983) suggest that there may be similar intra-population variation in the ratios of naturally-produced enantiomers of *exo*-brevicomin and response to them by *D. confusus*. Alternatively, these results might indicate that the beetles are responding to the natural enantiomer plus a kairomone (the unnatural enantiomer) produced by another beetle, advertising a suitable habitat.

One might expect significant inter-population variation in the pheromone of *D. confusus*, because the beetles' geographic range is so wide that environmental factors and the guild of sympatric species could vary greatly (Miller *et al.* 1989). In addition, relative amounts of cortical blister oleoresin components of subalpine fir have significant intra- and inter-population variation (Zavarin *et al.* 1970), which may indicate variation in availability of pheromone precursors, and a consequent potential for variation in the pheromone of *D. confusus* (Vanderwel and Oehlschlager 1987; Schlyter and Birgersson 1989).

The practical implication of response to both enantiomers is that for pest management one can use the racemic pheromone, instead of the naturally-produced (+)-enantiomer, which is very expensive to synthesize.

These results indicate that release rates from traps or trees are critical to the level of induced response. Thus, a release rate of < 0.8 mg/24 h of (±)-*exo*-brevicomin was insufficient to instill confidence that mass attack would occur on most baited trees. Increasing release rates resulted in increasing intensity of attack on baited trees, but the increase was not linearly proportional to the release rate. Rather, significant levels of induced attack appeared to depend on an approximate threshold of 0.8 mg/24 h, either from single or multiple sources (Tables 3.2.1-3 and 3.2.1-4). It is probable that this release rate is indicative of the number of beetles required to attack a tree successfully (Mulock and Christiansen 1986). Schlyter *et al.* (1987) suggest that attacking European spruce bark beetles are able to distinguish between trees releasing different levels of attractants, and that the discrimination is possible even when sources are only a few metres apart. My results suggest that *D. confusus* reacted similarly to the European spruce bark beetle, and would preferentially select trees in nature from which *exo*-brevicomin was being released at the highest rates.

A similar relationship in intensity of induced attack existed between release rates of *exo*-brevicomin from single trees and the numbers of trees baited in a spot (Tables 3.2.1-3 and 3.2.1-4). Baiting of five trees with a cumulative release rate of 2.0 mg/24 h produced a much more intensely concentrated beetle attack than baiting either 1 or 3 trees. Almost all baited trees were attacked, and 40% of these trees were mass attacked when 5 trees were baited (Table 3.2.1-4). It would be useful to know the effect of baiting varying numbers of trees per spot with a constant cumulative release rate of *exo*-breviciomin per spot.

The data from the 30 m strips clearly indicate that baiting trees with *exo*-brevicomin can concentrate new attack by within-stand populations within approximately 10 m of these trees, virtually eliminating beetle activity beyond 10 m, up to at least 30 m from these trees. This trend suggests that the highest release rate of *exo*-brevicomin was overriding any possible antiaggregation effects produced by colonizing beetles, and attracting enough beetles to cause switching of attack to nearby trees (Borden 1982a). Moreover, the 50 m inter-tree spacing used to concentrate and contain populations of the mountain pine beetle (Borden *et al.* 1983) is appropriate for semiochemical-based containment and concentration of *D. confusus* populations. No beetle could attempt to fly out of a stand without coming within 25 m of a baited tree, and populations would be well concentrated very close to baited trees, facilitating their subsequent management, e.g. extraction of small groups of infested trees. In future applied baiting programs it would be advantageous to ensure that the release rate of *exo*-brevicomin is always ≥ 0.8 mg/24 h per spot, and to bait more than one tree per spot. Baiting of two trees per spot, each with an *exo*-brevicomin release rate of 0.8 mg/24 h would meet these criteria, and is recommended for operational implementation.

3.2.2 *endo*-Brevicomin

3.2.2.1 Materials and methods

Beetle collection and maintenance. Beetle handling procedures followed those outlined by Stock and Borden (1983). Subalpine fir logs infested with *D. confusus* were collected from locations in interior British Columbia, waxed on each end to prevent dessication and stored outdoors in winter, or in a cold chamber at about 4° C. When beetles were required, infested logs were placed in screened emergence cages and held at about 20° C. Emerging beetles were collected daily, sexed by the presence (females) or absence of a setal brush on the frons (Bright 1976), and stored at 4° C on moistened paper towels in ventilated glass jars.

Laboratory bioassays. Enantiomers of *endo*-brevicomin were synthesized at Simon Fraser University to yield (+)-*endo*-brevicomin (99.7% chemical purity, 90% (+)- and 10% (-)- enantiomer), and (-)-*endo*-brevicomin (99.6% chemical purity, 91% (-)- and 9% (+)- enantiomer) (Oehlschlager and Johnston 1987). (±)-*exo*-Brevicomin (98.0% chemical purity) was supplied by Phero Tech, Inc., Delta, B.C. Male and female responses were tested to racemic *endo*-brevicomin and its enantiomers dissolved in pentane, alone or in combination with the attractive pheromone *exo*-brevicomin. Walking beetles were used for bioassays in an open arena olfactometer slightly modified from Wood and Bushing (1963), following procedures outlined by Stock and Borden (1983). Each stimulus (5.0 ng of *exo*-brevicomin; 5.0 ng of *exo*-brevicomin in combination with 2.5 ng of (+)-, (-)-, or (±)-*endo*-brevicomin; 2.5 ng of (+)-, (-)-, or (±)-*endo*-brevicomin) was tested with five groups of ten beetles of each sex.

Field trapping and baited tree experiments. Field studies were carried out in 1986 and 1987 in mature subalpine stands of the Bulkley and Morice Forest Districts in central British Columbia. Enantiomers of *endo*-brevicomin were tested in combination with (±)-*exo*-brevicomin. The release rate for both *endo*- and *exo*-brevicomin was approximately 0.2 mg per 24 h (determined in the laboratory for 24 h at 20° C, from two 1.0 mm internal diameter glass capillary tubes, contained in an open 400 ul polypropylene tube). Trapping experiments utilized eight-unit multiple funnel traps (Lindgren 1983), with a 50 m spacing between traps. Ten replicates in a randomized complete block design were conducted in 1986. The experiment was repeated with five replicates at each of two different locations in 1987.

A five-replicate baited tree randomized complete block experiment used apparently healthy subalpine fir trees ≥ 20 cm dbh, with 50 m between trees. Chemical release devices were placed in cardboard holders (Phero Tech Inc., Delta, B.C.), and affixed as high as possible on the north side of treatment trees, to avoid excessive exposure to sunlight, and consequent loss of chemicals. Trees were baited on 17 June 1986, and beetle attack was assessed on 20 August 1986 by peeling a 30 by 30 cm bark sample from the west side of each tree, and counting attack galleries. Samples were taken from the west side of trees to avoid the influence of direct sunshine on the southern aspect, which may reduce beetle attack density (Stock 1981), and to avoid bias due to the proximity of the chemical stimuli to the north. The experiment was repeated in 1987 with six replicates. Trees were baited on 6 June 1987, and beetle attack was assessed on 30 July 1987. The attractive control treatment was not tested in 1986 because of a shortage of (±)-exo-brevicomin.

Statistical Analysis. Analysis of variance was performed on the data from the first two experiments. The arcsine transformation was used on the percentage data from the bioassay experiment. A response of 10/10 (= 100%) was entered as 9.999991 to facilitate arcsine transformation. A response of 0 was entered as 0.000001, to avoid empty cells after arcsine transformation (Table 3.2.2-1). Analysis of the trapping and baited tree experiments was on data transformed using the square root of (x + (3/8)) (Zar

1984). Actual values are reported in Table 3.2.2-1. Actual means with back-transformed upper 95 % confidence limits are reported in Table 3.2.2-2, and for 1987 data in Table 3.2.2-3 (Sokal and Rohlf 1981). Actual means ± S.E. are reported for 1986 data in Table 3.2.2-3.

3.2.2.2 Results

Laboratory bioassays. Responses by both males and females to (+)-, (-)-, or (±)-*endo*-brevicomin were not significantly different from responses to the pentane control (Table 3.2.2-1). Combining (±)-*endo*-brevicomin with (±)-*exo*-brevicomin resulted in a response, for both sexes, that was significantly reduced from response to (±)-*exo*-brevicomin alone. This reduction in response was also obvious when (+)-*endo*-brevicomin was combined with (±)-*exo*-brevicomin, but not when (-)-*endo*-brevicomin was the combinant (Table 3.2.2-1). Thus, the (+) enantiomer of *endo*-brevicomin was the active component responsible for inhibition of response by *D. confusus* to *exo*-brevicomin, but the (-) enantiomer was inactive.

Field trapping and baited tree experiments. Catch of beetles was highest in traps baited with (±)-*exo*-brevicomin, or with a combination of (-)-*endo*-brevicomin and (±)-*exo*-brevicomin for all three repetitions of the experiment (Table 3.2.2-2). The catch was least when (±)- or (+)-*endo*-brevicomin was combined with (±)-*exo*-brevicomin, and in unbaited controls. This trend clearly suggests that the (+) enantiomer of *endo*-brevicomin inhibited beetle response to the attractant, and that the (-) enantiomer of *endo*-brevicomin was inactive, supporting laboratory bioassay results (Table 3.2.2-1).

The baited tree experiments confirmed laboratory and field trapping results. No attack occurred on untreated control trees, or on trees treated with (±)-*exo*-

Table 3.2.2-1. Bioassay response of *D. confusus* to enantiomers of *endo*-brevicomin in combination with racemic *exo*-brevicomin (50 beetles of each sex tested per stimulus).

Stimulus	Amount (ng/20 ul)	Percent Response[a]	
		Male	Female
(±)-*exo*-brevicomin	5.0	58a	84a
(±)-*exo*-brevicomin with (-)-*endo*-brevicomin	5.0 2.5	54a	80a
(±)-*exo*-brevicomin with (+)-*endo*-brevicomin	5.0 2.5	34b	32b
(±)-*exo*-brevicomin with (±)-*endo*-brevicomin	5.0 2.5	22bc	36b
(-)-*endo*-brevicomin	2.5	6c	2c
(+)-*endo*-brevicomin	2.5	4c	6c
(±)-*endo*-brevicomin	2.5	8c	0c
Pentane	20.0 ul	6c	0c

[a] Percents within columns, followed by the same letter, are not significantly different, Newman-Keuls multiple range test, $p \leq 0.05$.

Table 3.2.2-2. Catch of *D. confusus* in multiple funnel traps baited with (±)-*exo*-brevicomin in combination with enantiomers of *endo*-brevicomin in central British Columbia, 1986 and 1987.

	Catch per trap [Mean (upper 95% conf. limit)][a]		
Bait	1986	1987-1	1987-2
(±) *exo*-brevicomin	1.8 (2.73)a	2.0 (4.98)a	3.2 (8.00)ab
(±) *exo*-brevicomin with (–) *endo*-brevicomin	1.7 (2.56)a	1.5 (5.14)b	4.3 (14.5)a
(±) *exo*-brevicomin with (±) *endo*-brevicomin	Not tested	0.3 (1.06)b	0b
(±) *exo*-brevicomin with (+) *endo*-brevicomin	0.6 (1.34)ab	0b	0.4 (1.11)b
Blank control	0.2 (0.48)b	0b	0b

[a] Numbers within a column followed by the same letter are not significantly different, Newman-Keuls test, $p \leq 0.05$. Response to treatments not different between sexes, ANOVA, $p = 0.3978$ for 1986, $p = 0.1133$ for 1987-1, $p = 0.0854$ for 1987-2.

brevicomin in combination with (±)- or (+)-*endo*-brevicomin in 1986 (Table 3.2.2-3). All four trees treated with (-)-*endo*-brevicomin in combination with (±)-*exo*-brevicomin were attacked. Results of the 1987 experiment were similar, but for three of the six trees treated with (±)-*exo*-brevicomin (attractant) and (+)-*endo*-brevicomin (inhibitor) the effect of the attractant overcame the effect of the inhibitor, reducing the effect of the latter by half. In the two years together all 16 (100%) of the trees baited with (±)-*exo*-brevicomin alone or in combination with (-)-*endo*-brevicomin were attacked, whereas only three of 22 trees (13.6%) baited with (±)-*exo*-brevicomin plus either (+)- or (±)-*endo*-brevicomin were attacked. Thus, I am confident that these results again indicate that (+)-*endo*-brevicomin is an antiaggregation pheromone for *D. confusus*.

3.2.2.3 Discussion

Specific activity of chemical isomers, alone, or in some defined ratio of combination with their antipode, is now known to be common in insect chemical communication (Mori 1984). The demonstrated antiaggregative activity of (+)-*endo*-brevicomin (possibly in synergism with the (-) enantiomer, since the available enantiomeric compounds were not 100% pure) provides another example of this phenomenon.

Semiochemical-mediated termination of aggregation, which serves to optimize resource allocation by spacing of galleries, or by inducing beetles to switch their attack to nearby trees, is well documented among the Scolytidae (Wood 1982; Borden 1982a and 1982b; Borden 1985). Such "epideictic" pheromones (Prokopy 1981) may be released by either the responding or pioneer sex. There appear to be 3 main mechanisms by which attack termination and switching can occur (Birgersson 1988): (1) the release rates of multifunctional pheromones may increase, crossing the threshold from attractiveness to repellency; (2) release rates of attractive pheromones may decline to insignificant levels

Table 3.2.2-3. Attack by *D. confusus* on *A. lasiocarpa* baited with racemic *exo*-brevicomin in combination with enatiomers of *endo*-brevicomin, 1986.

Year	Bait	Number of trees		No. of attacks per m^{2a} (mean ± SE, 1986) [Mean (upper 95% conf. limit), 1987]
		Treated	Attacked	
1986	(±)-*exo*-brevicomin with (±)-*endo*-brevicomin	5	0	0
	(±)-*exo*-brevicomin with (+)-*endo*-brevicomin	5	0	0
	(±)-*exo*-brevicomin with (−)-*endo*-brevicomin	4	4	16.7 ± 11.44
	Blank control	5	0	0
1987	(±)-*exo*-brevicomin	6	6	192.3 (339.67)a
	(±)-*exo*-brevicomin with (±)-*endo*-brevicomin	6	0	0b
	(±)-*exo*-brevicomin with (+)-*endo*-brevicomin	6	3	88.9 (206.67)ab
	(±)-*exo*-brevicomin with (−)-*endo*-brevicomin	6	6	164.4 (317.0)a
	(±)-*endo*-brevicomin	6	0	0b
	Blank control	6	0	0b

[a] Numbers followed by the same letter are not significantly different, Newman-Keuls test, $p \leq 0.05$.

following mating or (3) a qualitatively different antiaggregation pheromone may be produced following mating.

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It may be the absolute amount of *endo*-brevicomin that imparts antiaggregation activity. Thus, one male producing an 18:1 ratio of *exo*- to *endo*-brevicomin may induce aggregation. However, 100 males might produce enough *endo*-brevicomin to terminate an attack, or to cause switching of hosts, regardless of the amount of attractive *exo*-brevicomin they produce. The multifunctional pheromone MCH is attractive to the Douglas-fir beetle at low concentrations, but functions as an antiaggregation pheromone at high release rates (Rudinsky 1973). Alternatively, the ratio of *endo*- to *exo*-brevicomin may change. The initially attractive ratio of verbenone: *cis*-verbenone emmitted from galleries of attacking male European spruce bark beetles changes from 1:10 to 1:1 at the end of 7 days (Birgersson and Birgstrom 1989). In this case, part of the increase in verbenone released could occur because it is produced from verbenols and pinenes by microorganisms which become established in the gallery wall and phloem (Leufven *et al.* 1984).

Among polygamous species, pine engravers and European spruce bark beetles appear to utilize an internal feedback mechanism which weakens the male pheromone signal as mating occurs with successive females (Borden 1967; Byers 1981). A similar phenomenon occurs with the smaller European elm bark beetle. This could possibly occur with *D. confusus* (Borden 1987b), although Stock and Borden (1983) found no significant reduction in the attraction of females to extracts of mated males. Byers (1981) notes that a post-mating decline in the release of attractant pheromone may not be sufficient to terminate mass-attraction, because continued arrival of unmated pioneering beetles would sustain the release of attractants.

It may be that a qualitatively different pheromone is produced to terminate aggregation; it has been shown that mated female *D. confusus* may produce an antiaggregation pheromone (Stock and Borden 1983).

Until now, *endo*-brevicomin has been reported to have antiaggregative activity only in the southern pine beetle and the mountain pine beetle (Borden 1987a). The demonstration that the antiaggregation pheromone (+)-*endo*-brevicomin is produced by *D. confusus* should prompt further research to resolve which mechanism(s) is used by *D. confusus* to terminate mass attack and/or initiate switching to another tree. In addition, just as verbenone can be operationally used to suppress attack by the mountain pine beetle (Amman *et al.* 1989; Lindgren *et al.* 1988b), there is potential for the use of *endo*-brevicomin for manipulating *D. confusus* populations in infested subalpine fir stands.

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4. SEMIOCHEMICAL-BASED MANAGEMENT OF *DRYOCOETES CONFUSUS*.

4.1 INTRODUCTION

4.1.1 Semiochemical-based management of scolytids.

The discovery that semiochemical-based communication is crucial in the biology of many insect pests has led to much research focused on utilizing this knowledge in pest management. In a recent review, Borden (1989) examined the semiochemical communication system of scolytids for points of vulnerability, and explained how these points can be exploited in scolytid management. The following, based on Borden (1989, 1990), briefly summarizes current semiochemical-based management practices for scolytids.

Exploitation of primary attraction. Some scolytid species, e.g. the spruce beetle (Nagal *et al.* 1957, Schmid and Frye 1977), the European spruce bark beetle (Bakke 1989), and the Douglas-fir beetle (Rudinsky 1966, McMullen 1977) show a marked preference for moribund host material such as freshly felled trees. Primary attraction to such a host results in an incipient infestation, which in turn results in the production of a very powerful secondary attraction. This natural attraction can be superior to that produced when healthy standing trees are baited with aggregation pheromone (Dyer and Safranyik 1977). Thus, deliberately felled trees can be used as population sinks that are removed once infested, or made lethal with topical or systemic applications of insecticides (Heath 1980).

Prevention of attack. Prevention of attack and subsequent pheromone production resulting in mass attacked trees can be accomplished through removal or manipulation of susceptible host materials. Sanitation logging to remove susceptible host types and incipient infestations is commonly used to control mountain pine beetle (Amman *et al.* 1977, McMullen *et al.* 1986). Rapid turnover of stored log inventory is recommended for control of ambrosia beetles (Borden 1990), and careful management of log decks at landings and along roads is useful in preventing the buildup of populations of spruce beetle (Schmid and Frye 1977) and the Douglas-fir beetle (McMullen 1977). Thinning of lodgepole pine stands appears to result in conditions that are unfavourable for mountain pine beetle (Bartos and Amman 1989). Topical application of insecticides (Berisford *et al.* 1982, Hall *et al.* 1982, Werner *et al.* 1986), or of repellents such as pine oil (Nijlholt *et al.* 1981), can protect host materials from attack.

Disruption of olfactory perception. Saturation of an area with semiochemicals can produce sensory adaptation or habituation which results in the failure of beetles to respond in a natural manner (Tilden *et al.* 1981). Thinning of lodgepole pine stands may produce within-stand conditions that are unfavourable to the development of pheromone plumes, effectively disrupting pheromone perception (Bartos and Amman 1989).

Exploitation of secondary attraction. Mass trapping of beetles by baiting various types of traps with aggregation pheromones has been attempted against the western pine beetle (Bedard and Wood 1981), ambrosia beetles (Lindgren and Borden 1983), the smaller European bark beetle (Lanier 1979), and the European spruce bark beetle (Bakke 1989). Programs dealing with relatively small, isolated populations seem to have the best success (Borden 1990). Containment and concentration of beetle attack in and around trees baited with aggregation pheromones to control within-stand distribution of beetle attack, and/or prevent population dispersal to other areas has been used with considerable success against the mountain pine beetle (Borden 1990). Standing baited trees can also be treated with topical or systemic applications of insecticides to create lethal population sinks (Borden 1990). Secondary attractants can be used to monitor beetle flights to time treatments such as chemical applications, to minimize the risk of spreading populations during transport of infested logs (Stock 1984), or to monitor population size and trends (Vité 1984; Bakke 1985; Bakke 1989).

Exploitation of antiaggregation pheromones. Antiaggregation pheromones have been used to prevent beetle attack by bark beetles on individual trees and in stands. The multifunctional pheromone MCH is attractive to the Douglas-fir beetle at low concentrations, but functions as an antiaggregation pheromone at high release rates (Rudinsky 1973). MCH has been used successfully to reduce attacks by the Douglas-fir beetle and the spruce beetle on felled trees when applied directly to trees (Kline *et al.* 1974; Lindgren *et al.* 1988a, 1989), or in broadcast aerial applications (McGregor *et al.* 1984). Similarly, the antiaggregation pheromone verbenone has been used to reduce mountain pine beetle attack in infested stands (Amman *et al.* 1989, Lindgren *et al* 1988b), and has been shown to reduce southern pine beetle attacks (Richerson and Payne 1979).

4.1.2 Semiochemical-based management of *Dryocoetes confusus*.

Any pest management strategy, including effective use of semiochemicals, requires an adequate knowledge of the biology of the target organism. Mathers (1931) described a two year life cycle for *D. confusus* in B.C. The first emergence of new adults occurred in late June, and continued throughout July. These adults attacked fresh host material, with the attacking polygynous males excavating nuptial chambers, and mating with up to four females (Bright 1976). Females excavated brood tunnels and layed eggs until "well into August" (Mathers 1931). Eggs were laid on both sides of the females' galleries. After egg laying was completed the parent adults extended brood tunnels by feeding, creating tunnels in which they overwintered. The following spring, females laid a second brood in a continuation of these same tunnels. Parents then re-emerged in mid-July to attack fresh material, and lay a third brood. Eggs of the first brood apparently hatched in late August, overwintered as small larvae, developed to teneral adults, and overwintered again, emerging at the beginning of the next (third) summer. Thus, the life cycle in B.C. is usually two years. Bright (1963) suggested that the life cycle is completed in one year or less in the western and southwestern United States.

Some of the knowledge of *D. confusus* attack habits and semiochemical-based communication suggests potential for applications in pest management. My observations suggested that *D. confusus* in British Columbia will readily infest subalpine fir windfalls in the forest and around cut block edges, in much the same manner as does the spruce beetle (Bright 1976), and that these infestations may expand to nearby healthy standing trees. It has been demonstrated that (±)-*exo*-brevicomin can be used to induce attack on standing trees (Borden 1987b, Chapter 3), and that (+)-*endo*-brevicomin is an effective antiaggregation pheromone (Chapter 3). Thus, both *exo-* and *endo*-brevicomin have excellent potential for manipulating western balsam bark beetle populations.

4.1.3 **Objectives**

My objectives were to:

1. describe the seasonal flight patterns of *D. confusus*, and to assess the vertical distribution of within-stand flight,
2. assess the effectiveness of the aggregation pheromone *exo*-brevicomin for containment and concentration of beetle populations within infested stands,
3. confirm that *D. confusus* preferentially attacks freshly felled logs, and
4. to test the effectiveness of *endo*-brevicomin for preventing attack on felled trees, and for reducing attack in stands with active infestations.

4.2 FLIGHT HABITS

4.2.1 Material and methods

Eight-unit multiple funnel traps were set out at different locations in the Bulkley Valley, in north-central B.C., annually from 1985 - 1987. Trapping periods and locations were 19 June - 22 Aug., 1985, at Gramaphone Creek, 13 June - 27 August, 1986, at Gramaphone Creek, and 28 May - 27 August, 1987, at Kwun Creek. The traps were suspended on ropes between two non-host or uninfested subalpine fir trees in stands with current beetle infestations, and were at least 50 m apart. The top of each trap was 2 m above ground in 1985 and 1986, and 3 m in 1987. Attractive bait in each trap was the aggregation pheromone (±)-*exo*-brevicomin (Albany Intl., Columbus, Ohio), 99.7% purity (Conn *et al.* 1983; Borden *et al.* 1987b), in 2 glass capillary tubes, collectively releasing 0.4 mg/24 h in 1985 and 1986, and (±)-exo-brevicomin (Phero Tech Inc., Delta, B.C.) 98% purity, 4 capillary tubes, collectively releasing 0.8 mg/24 h in 1987. Captured *D. confusus* were counted and sexed daily in 1985, and Monday, Wednesday, and Friday in 1986 and 1987. Within-stand temperature and relative humidity patterns were monitored with a hygrothermograph (C.F. Casella and Co., London, UK, Model 3083/TT) placed in a Stevenson screen located under the canopy directly on the ground near the funnel traps.

In a separate experiment in 1986, 10 *exo*-brevicomin-baited traps spaced 50 m apart were set out at Gramaphone Ck.. Five randomly selected traps were suspended approximately 2 m above ground, and 5 were suspended approximately 6 m above ground, from 19 June to 11 July.

Degree days were calculated from the hygrothermograph data for a lower threshold of 5° C, using the method outlined by Baskerville and Emin (1969). The average degree day accumulation per day starting from the first day of sampling was calculated for the entire flight sampling period each year (Number Cruncher Statistical System 1988). Degree day accumulation per 3-day interval was calculated and plotted together with total beetle catch for the same interval over time for the entire sampling period each year, and presented in graphical form (Fig. 4.2-1). Data from the trap height experiment were compared using a t-test (Number Cruncher Statistical System 1988).

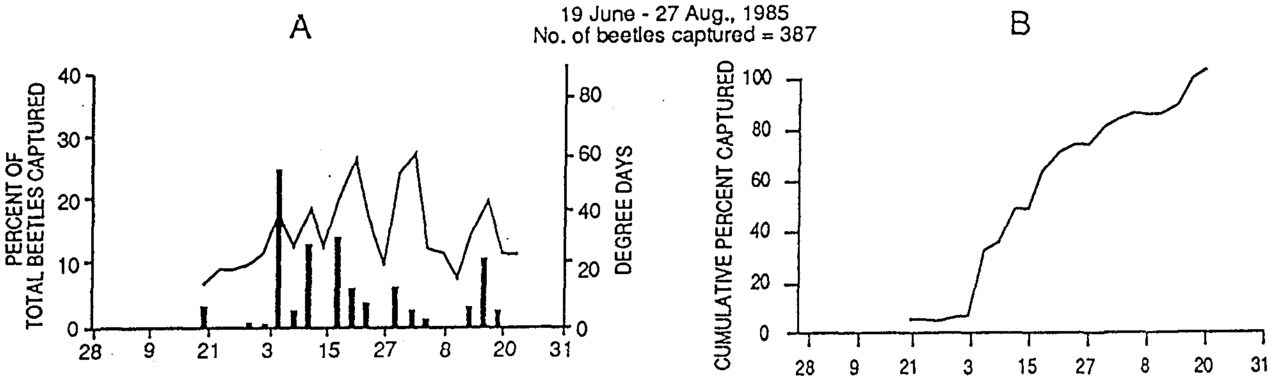
4.2.2 Results

Seasonal flight patterns (Fig. 4.2-1a) indicated that *D. confusus* has at least two flight periods each summer, confirming Mathers' (1931) findings. The first (main) flight period was in mid- to late June, and the second in mid-August. Flight had probably started prior to trap placement in 1985 and 1986, because beetles were caught in the first collection period. The trends for cumulative captures were roughly similar each year, a slow rise followed by a sharp increase, with the pattern then repeating itself (Fig. 4.2-1b). By assuming a separation of the two flights on 1 August, the second flight represented 18.7 %, 16.7 %, and 26.1 % of total flight in 1985, 1986, and 1987, respectively. Flight apparently commenced in early June, 1987 (Fig. 4.2-1a), but was stopped by a period of low temperature. Some flight occurred in September in all years (pers. obsv.), after the traps had been taken down.

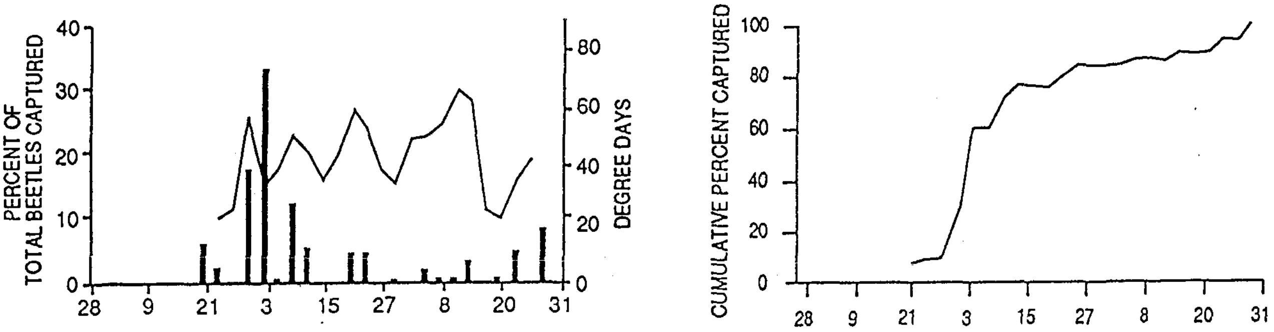
Very little flight occurred when daily maximum temperatures within stands were < 15° C. Some flight occurred at temperatures considerably below 15° C; however this may have been influenced by the placement of the Stevenson screen on the ground, where temperatures may have been cooler than temperatures in the canopy (Fig. 4.2-2). Peaks in flight activity occurred between 16 and 26° C, coinciding with peaks in accumulated degree days (Fig. 4.2-1a). Very little flight occurred in the interval between flight periods, despite apparently adequate degree day accumulations (Fig. 4.2-1b).

Figure 4.2-1. Seasonal flight patterns (bar graph) and degree day accumulations (solid line) above 5° C (A), and cumulative flight patterns (B), in 3-day intervals, for *D. confusus* trapped in (±)-*exo*-brevicomin-baited multiple funnel traps at Gramaphone Ck., B.C., 1985-1986, and Kwun Ck., B.C., 1987.

19 June - 27 Aug., 1985
No. of beetles captured = 387



13 June - 27 Aug., 1986
No. of beetles captured = 233



28 May - 27 Aug., 1987
No. of beetles captured = 832

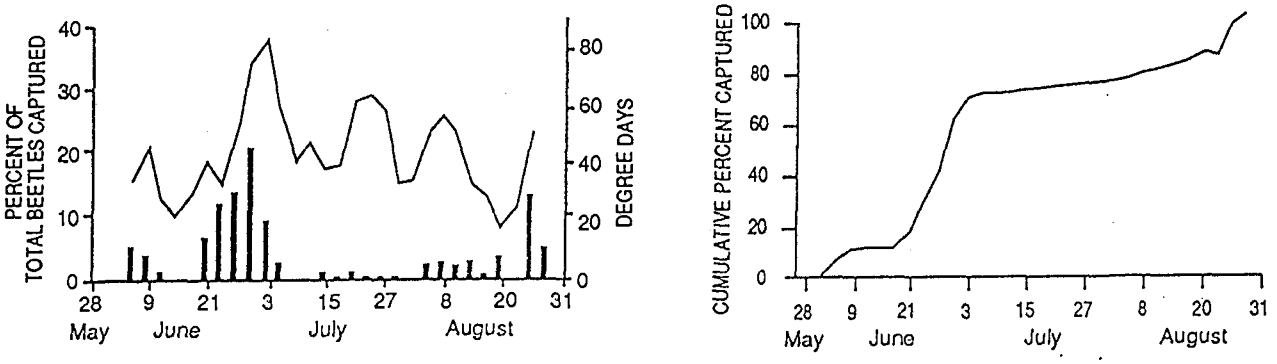
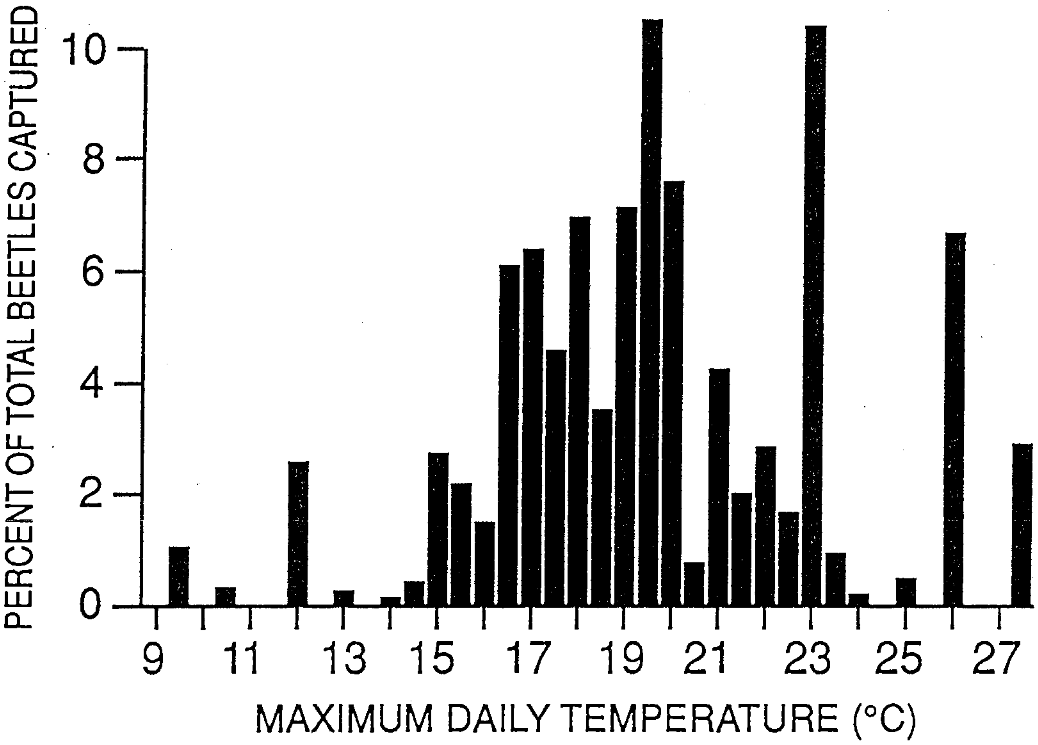


Figure 4.2-2. Relationship between within-stand daily maximum temperature and flight of *D. confusus* populations in central B.C., 1985 - 1987.


PERCENT OF TOTAL BEETLES CAPTURED
10
8
6
4
2
0
9
11
13
15
17
19
21
23
25
27
MAXIMUM DAILY TEMPERATURE (°C)

Average degree-day accumulation per day was 11.5 ± 0.63 in 1985, 14.3 ± 0.60 in 1986, and 14.3 ± 0.64 in 1987. The low accumulation per day in 1985 could possibly explain the short interval between flight peaks; cooler weather would have resulted in longer development times and fewer windows for flight (Figs. 4.2-1, 4.2-2).

More males were caught early in the season, and the sex ratio became progressively female-biased over time (Fig. 4.2-3). The ratio of males to females in the first flight (up to August 1) was 1.1 in 1985, 2.4 in 1986, and 1.0 in 1987. In the second flight the ratio of captured males to females was 0.2 in 1985, 1.1 in 1986, and 0.34 in 1987. Fewer beetles caught in 1986 than in other years probably resulted in less clearcut trends.

Approximately four times more beetles were captured in traps at the 6 m height than at 2 m (Table 4.2-1).

4.2.3 Discussion

Clear sunny days with no precipitation, high vapour pressure deficits, and high incident net radiation resulting in high evapo-transpiration rates are characteristic of late June and early July in subalpine forests (Alexander 1987). Seasonal moisture deficits may be correlated to maximal host susceptibility to bark beetle attack, and main scolytid flight periods may occur during these periods. The evidence that the main flight period of the western balsam bark beetle occurs primarily in mid- to late June suggests this correlation, and corresponds well with Mathers' (1931) data on life history, although it is clear that flight can begin in early June (Fig. 4.2-1). The occurrence of the second peak in mid-August, however, was one month later than the mid-July reemergence described by Mathers (1931). This apparent delay may be due to the fact that Mathers (1931) studied beetles emerging from caged subalpine fir bolts at Stanley, B.C., approximately 1.5°

Figure 4.2-3. Seasonal variation in male component of flying *D. confusus* populations, Gramaphone Ck., B.C., 1985-1986, and Kwun Ck, B.C., 1987.

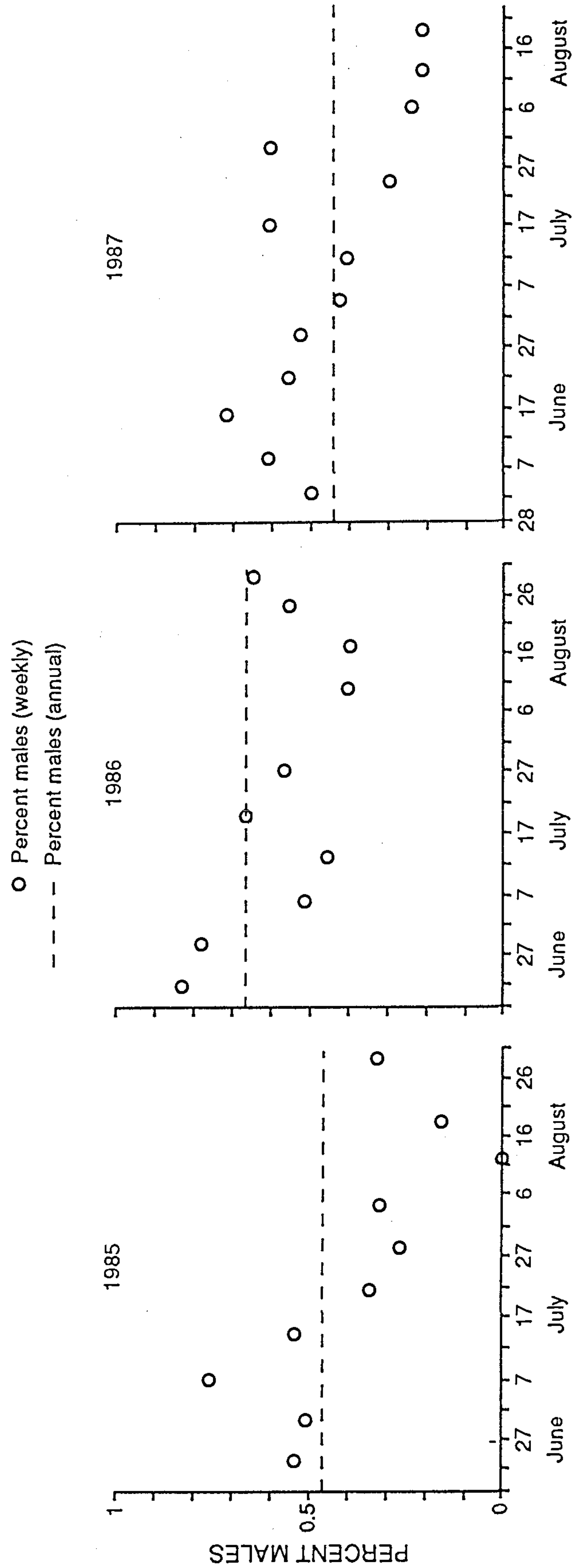

PERCENT MALES
1
0.5
0
1985
1986
1987
June
July
August
27
7
17
27
6
16
26
28
○ Percent males (weekly)
- - - Percent males (annual)

Table 4.2-1. Catch of *D. confusus* in a 5-replicate experiment in which (±)-*exo*-brevicomin baited 8-unit multiple funnel traps were placed at 2 and 6 m ht above ground, June 19 - July 11, 1986, Gramaphone Ck. B.C.

	No. of beetles per trap (Mean ± S.E.)[a]	
Trap height	Males	Females
2 m	15 ± 3.0a	5 ± 1.8a
6 m	49 ± 9.8b	29 ± 7.2b

[a] Means within columns followed by the same number are not significantly different, t-test, $p \leq 0.025$.

latitude south of the Bulkley Valley (Canada Min. Energy, Mines, and Resources 1980; Canada Dept. Mines and Technical Surveys 1957). One would expect warmer weather as one proceeds southward, and more rapid development of beetle broods (Stock 1981). Weather-dependent variation in the length of life cycles is common within scolytid species (Amman 1973; Schmid and Frye 1977; Langor 1987). Further investigations are required to discover if *D. confusus* can indeed develop on a one-year cycle, as suggested by Bright (1963), a characteristic that could become more prevalent under conditions of global warming. It is essential to understand variability in life cycle duration and flight periods in order to implement pest management tactics, e.g. semiochemical-based population manipulation, effectively.

The period between flight peaks would correspond to the period when females in galleries are laying a second brood (Mathers 1931) and/or feeding to regenerate their flight muscles (Chapman 1957; Borden and Slater 1968; Bhakthan *et al.* 1970; Bhakthan *et al.* 1971). Exact information on when first, second, or third brood beetles are represented in flying populations at higher latitudes at any given time of the year awaits further study.

There was no evidence for an early emergence of the responding sex (females) (Fig 4.2-3), considered to be an outbreeding mechanism in other scolytids (Cameron and Borden 1967; Billings and Gara 1975; Borden 1982a). Rather, data suggest an early emergence of the pioneering sex (males) (Fig. 4.2-3). A similar pattern can occur for emerging summer brood of the European spruce bark beetle (Botterweg 1983; Anderbrandt 1989) It is quite possible that in old growth subalpine forests, the patchy and temporary nature of the host resource (newly-susceptible or freshly-downed trees) may force neighbouring beetle populations to search overlapping areas. Early emerging males could establish new attraction centres resulting in multiple matings with females from different populations, and enhance the genetic heterogeneity of their progeny

(Flamm *et al.* 1987). If the responding sex were to emerge first in such a harsh environment, the uncertainty of initial attack success, establishment of secondary attraction, and ultimately mass-aggregation (Borden *et al.* 1986) could be increased, resulting in high mortality of the responding sex during dispersal. Subsequent reemergence and flight of females late in the summer (Fig. 4.2-3) may enhance genetic heterogeneity of the population if they were to migrate significant distances from their original host tree (Cameron and Borden 1967).

I conclude that a significant proportion of the second flight is comprised of reemergent adults, probably females Mathers 1931). Flamm *et al.* (1987) found that 75 and 64 %, respectively, of attacking *Ips avulsus* Eichoff and *Ips calligraphus* Germar reemerged from original host trees, and that males represented only 27.8 % of reemergent *I. avulsus* vs. 46.7 % of reemergent *I. calligraphus.* Anderbrandt *et al.* (1985) found that about 84 % of European spruce bark beetles reemerged, of which about 36 % were males. Potential growth of a population is enhanced when progeny beetle numbers are augmented by reemerging adults exploiting unused bark in previously attacked but not fully utilized trees, or even attacking new trees (Flamm *et al.* 1987; Paine *et al.* 1988). Also, those females fit enough to reemerge may gain an adaptive advantage by producing a second or third set of progeny (Flamm *et al.* 1987). In any pest management strategy it would be important to extend the duration of pest management tactics to include the period when these reemerged, and presumably gravid females (Stock 1981; Anderbrandt 1989) are active.

It is common for scolytids to exhibit flight patterns which presumably avoid the impediments of understory vegetation and dense tree crowns, and are positioned to intercept pheromone plumes (Ashraf and Berryman 1969; Schmitz *et al.* 1980; Amman and Cole 1983; Forse and Solbreck 1985; Bartos and Amman 1989). This is supported by the higher catches in traps at 6 m than at 2 m ht (Table 4.2-1). Understory vegetation can be 3 or 4 m high in subalpine forests. For semiochemical-based manipulation of *D. confusus* populations it would be useful to know what relationship this flight pattern might have to the initial attack height and vertical distribution of attack density by *D. confusus* on standing trees.

4.3 CONTAINMENT AND CONCENTRATION OF INFESTATIONS WITH *EXO*-BREVICOMIN

4.3.1 Materials and methods

A four replicate experiment in 1986 consisted of paired 9 ha forest blocks (300 x 300 m) with current balsam bark beetle infestations. Three of the replicates were in the Miner Creek drainage of the Merritt Forest District, and the fourth replicate was located near Nata Creek, in the Bulkley Forest District, B.C. Blocks within each pair were between 100 and 200 m apart. In the treated blocks, 36 apparently healthy trees ≥ 20 cm diameter at 1.3 m ht (dbh) were selected at 50 m centres. Selected trees were marked with paint and baited with 2 capillary tubes (1.0 mm i.d.) collectively releasing *exo*-brevicomin released at 0.4 mg/24 h, in cardboard holders (PheroTech Inc., Delta., B.C.) which were stapled to the north side of trees on 1-15 June 1986 prior to the onset of beetle flight. This layout resulted in an application rate of 4 baits per ha, and therefore, any beetles emerging within or flying through the stand had to pass within 25 m of a baited or marked tree (Borden *et al.* 1983). Selected trees at 50 m centres in the control blocks were clearly marked with paint, but left unbaited.

All 9 ha blocks were 100 % surveyed for balsam bark beetle attack in September-October, 1986, using procedures outlined in Borden (1983). Three categories were used to classify attacked trees. Trees which had been attacked in previous seasons, and presumed to contain live beetle brood were classified as "red" if, in the judgement of the surveyors, such trees retained enough red foliage that they could be identified from aerial surveys. Attacked trees with fresh resin streams on the bole, but no other sign of attack, were considered to have repelled beetle attack. Trees with fresh boring dust on the bole, and/or on the ground around the base of the tree were considered to have been mass attacked. The dbh and (x,y) coordinate position was recorded for all baited, marked and attacked trees within each block.

A second experiment was carried out in 1987 with five replicates of paired 16 ha forest blocks. Three replicates were located in the Miner Creek drainage of the Merritt Forest District, and two replicates were located in the Telkwa River drainage of the Bulkley Forest District. Blocks within each pair were 200 m apart. A 4 ha zone (200 x 200 m) was laid out within the centre of each block, and at 50 m intervals 2 healthy subalpine fir > 20 cm dbh were selected. In the treated blocks each selected tree was baited as above with 4 capillary tubes collectively releasing *exo*-brevicomin at 0.8 mg/24 h, on 1-15 June 1987. Selected trees in the control blocks were clearly marked with paint, but left unbaited. In all blocks the 12 ha area outside the central zone (referred to as the "peripheral zone") was untreated.

Assessment of the 16 ha block experiment was carried out as described above in September-October 1987. Due to time and resource constraints one of the Telkwa River replicates, and one treated and one control block of the Miner Creek replicates were surveyed over only half their area (8 ha).

Statistical analysis. For both experiments, diameters of baited or marked trees were compared between treatments using the Kolmogorov-Smirnov 2-sample test (Systat 1988).

Nearest neighbour distance methods have been commonly applied in analysis of the spatial distribution of plant populations to identify competitive effects. To the best of my knowledge, distance methods are not often used in studies of semiochemical-based management of scolytids although there has been assessment of spatial patterns of beetle galleries within trees (Shepherd 1965; Nilssen 1978; Byers 1984). Most assessments of semiochemical-based management studies have utilized counts or ratios of change as empirical measures of the effectiveness of treatments, despite the fact that "examination of the quantity of beetle attacks and the probable location of the source of attacking beetles are better measures of the success of concentration and containment objectives" than simple tree counts (Gray and Borden 1989). The use of distance techniques, while time consuming, can provide a much more detailed picture of the spatial arrangement of scolytid populations.

Lotus 1-2-3 (TM) macro programs (Appendix II) were written to calculate nearest neighbour distances using the (x,y) coordinates of trees. Nearest neighbour distances between all newly-mass attacked trees, red trees, newly-mass attacked trees and red trees, red trees and baited or control trees, and newly mass attacked trees and baited or control trees were compared between treatment and control blocks using a non-parametric equivalent to a two-way analysis of variance (Friedmans test; Systat Inc., 1988). Nearest neighbour distances were also used in a macro program written to calculate the Clark-Evans test for spatial randomness (Clark-Evans statistic) with corrections for edge effect (Clark and Evans 1957; Donnelly 1978) for all mass-attacked and red trees in each block. The Clark-Evans statistic measures the extent to which the density of mapped points varies from place to place within a sampled area, and is compared to the *Z*-value for normal distributions. Clark-Evans statistic values of less than 0 indicate a tendency towards an aggregated distribution of mapped points, and positive values indicate a tendency towards a regular pattern of points. The statistic is considered a simple but powerful test for spatial randomness of points distributed in 2 dimensions (Sinclair 1985). Friedmans test (Systat 1988) was used to compare count and distance data, and the Clark-Evans statistic.

The percentage of nearest neighbor distances between marked trees and newly mass-attacked trees that were within 10, 20, 30, 40, and ≥ 40 m were compared between treatment and control blocks in the 9 ha experiment using the G-test (Zar 1984).

For both experiments, counts of attacked trees per ha were compared between treatments using the G-test for the entire block in the 9 ha experiment, and for the central and peripheral zones in the 16 ha block experiment. The percentage of all mass attacked trees in the stand that occurred in the year of treatment, the "percentage change", was calculated as:

$$\frac{(\text{number of mass attacked trees/ha})(100)}{(\text{number of mass attacked trees/ha} + \text{number of red trees/ha}).}$$

4.3.2 Results

Nine ha Experiment. Diameters in two of the three baited 9 ha blocks were significantly higher than in the control blocks (Table 4.3-1).

There were no significant differences in the numbers or pattern of red trees between treated and control blocks in the 9 ha experiment (Table 4.3-2). Mean nearest neighbour distance between red trees was approximately 6 m, and approximately 87 % of all nearest neighbours were ≤ 10 m apart (Fig. 4.3-1a). The Clark-Evans statistic was -11.7 for both baited and control blocks, indicating a strongly aggregated spatial distribution of red trees ($p < 0.0001$). The distribution of red trees around baited or marked trees was identical for both treatments (Fig. 4.3-1b).

There were significantly more newly mass-attacked trees in the baited (103 of 143 baited trees) than in the control blocks (2 of 143 marked trees) (Table 4.3-2). The percentage change was significantly lower in control blocks. Low levels of beetle activity resulted in very few mass attacks in three of four control blocks (Table 4.3-2). Consequently, no statistical comparisons were made between treatments for nearest neighbour distances, the Clark-Evans statistic, or distance to the nearest red tree for newly mass-attacked trees. The Clark-Evans statistic for mass attack was not significantly different from a random distribution in the treated block ($p = 0.1814$, Table 4.3-2). Mean nearest neighbour distance between mass attacks was greater in the

Table 4.3-1. Numbers and diameters of baited or marked trees at 1.3 m above the root collar (dbh) for 9 and 16 ha baited block experiments, 1986 and 1987.

Replicate and location	Number of trees		Diameters at dbh (cm) (Mean ± SE)		Probability of significant difference between baited and control blocks [a]
	Baited blocks	Control blocks	Baited blocks	Control blocks	
9 ha block experiment (1986)[b]					
1. Prospect Creek	34	36	44 ± 1.6	38 ± 1.4	*
2. Prospect Creek	35	34	37 ± 0.9	35 ± 1.1	NS
3. Prospect Creek	33	33	33 ± 0.9	25 ± 0.8	*
16 ha block experiment (1987)					
1. Prospect Creek	15	29	42 ± 4.5	40 ± 2.0	NS
2. Prospect Creek	29	28	42 ± 2.4	37 ± 2.3	*
3. Prospect Creek	31	21	38 ± 1.6	41 ± 2.3	NS
4. Telkwa River	31	30	36 ± 1.9	40 ± 1.6	*
5. Telkwa River	16	16	31 ± 1.7	37 ± 2.4	NS

[a] * = $P \leq 0.05$, NS = not significant, Kolmogorov-Smirnov test for 2 samples (Systat 1988).

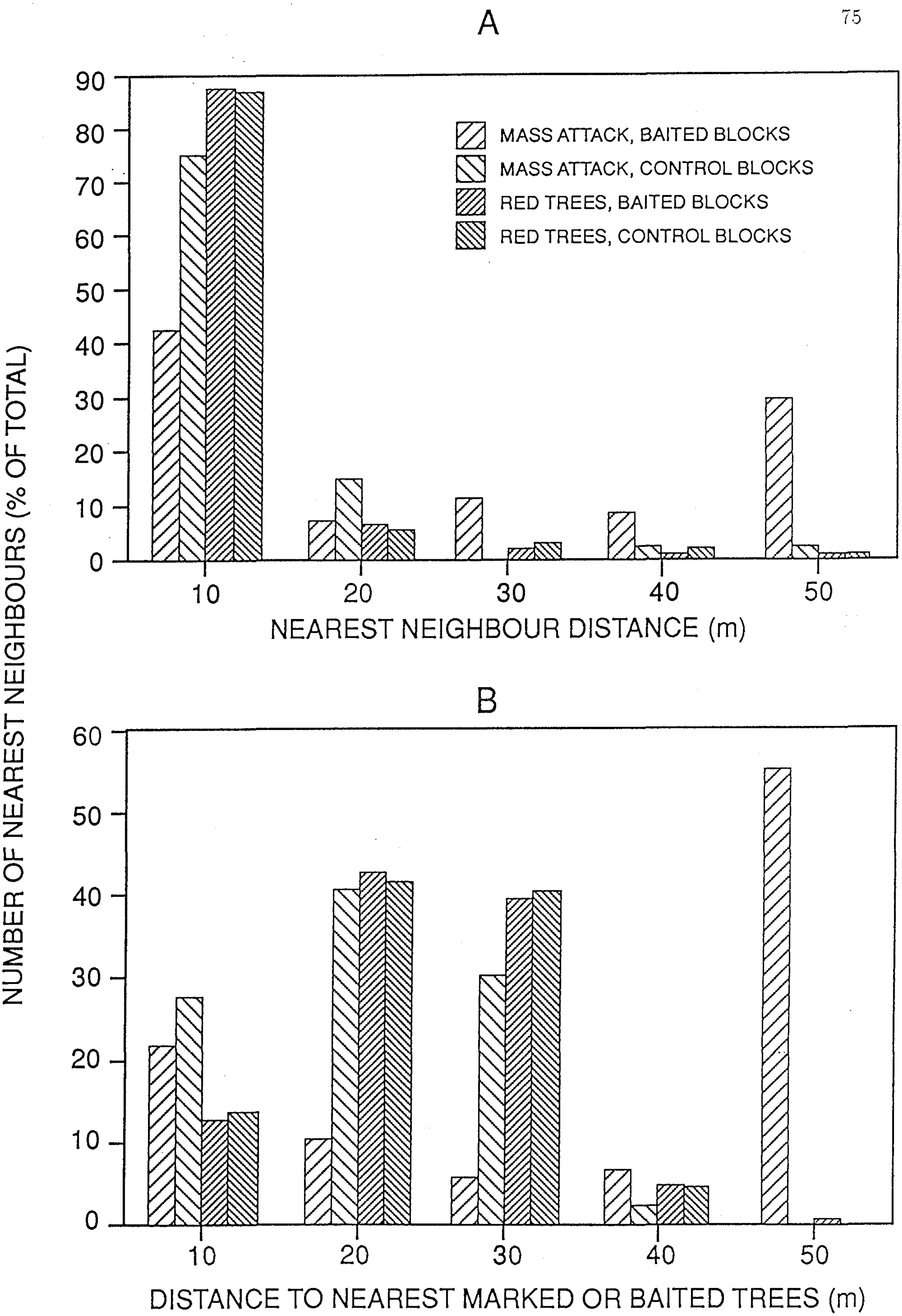
[b] No data for Nata Ck. replicate.

Table 4.3-2. Analysis of the spatial pattern of trees attacked by *D. confusus* in paired baited and control 9 ha blocks with (±)-*exo*-brevicomin baits applied to trees over a 50 m grid spacing in the treated blocks (n=4).

	Red trees[a]			Newly mass-attacked trees [a]		
Criteria assessed	Baited blocks (Mean ± SE)	Control blocks (Mean ± SE)	Probability of significant difference between baited and control blocks	Baited blocks (Mean ± SE)	Control blocks (Mean ± SE)	Probability of significant difference between baited and control blocks
No. trees per ha	13.6 ± 1.2	16.1 ± 4.0	NS	5.1 ± 1.0	1.3 ± 1.1	*
Nearest neighbour (m)	5.8 ± 0.5	6.3 ± 1.0	NS	23 ± 3.5	10.3	NA
Clark-Evans statistic	-11.7 ± 0.9	-11.7 ± 1.6	NS	-0.91 ± 1.0	-6.69 ±	NA
% change	-	-	-	40.6 ± 3.2	5.8 ± 3.5	*
Nearest red tree to (m)	-	-	-	22.8 ± 14.4	7 ± 1.0	NA
Nearest baited or marked tree (m)	24 ± .07	24.5 ± 3.2	NS	36.5 ± 5.1	43 ± 4.1	NA

[a] Friedmans test (Systat 1988) used for analysis of distance and count data and Clark-Evans statistic, G-test (Zar 1984) used for comparison of percentage data. * = $p \leq 0.05$, NS = not significant, NA = no analysis computed because of a lack of newly mass-attacked trees in 3 of 4 control blocks.

Figure 4.3-1a,b. Distribution of nearest neighbour distances (A) and distances to nearest marked or baited tree (B) for trees attacked by *D. confusus* in paired baited and control 9 ha blocks. Baited trees with *exo*-brevicomin released at 0.4 mg/24 h applied to trees over a 50 m grid, interior British Columbia, 1986.

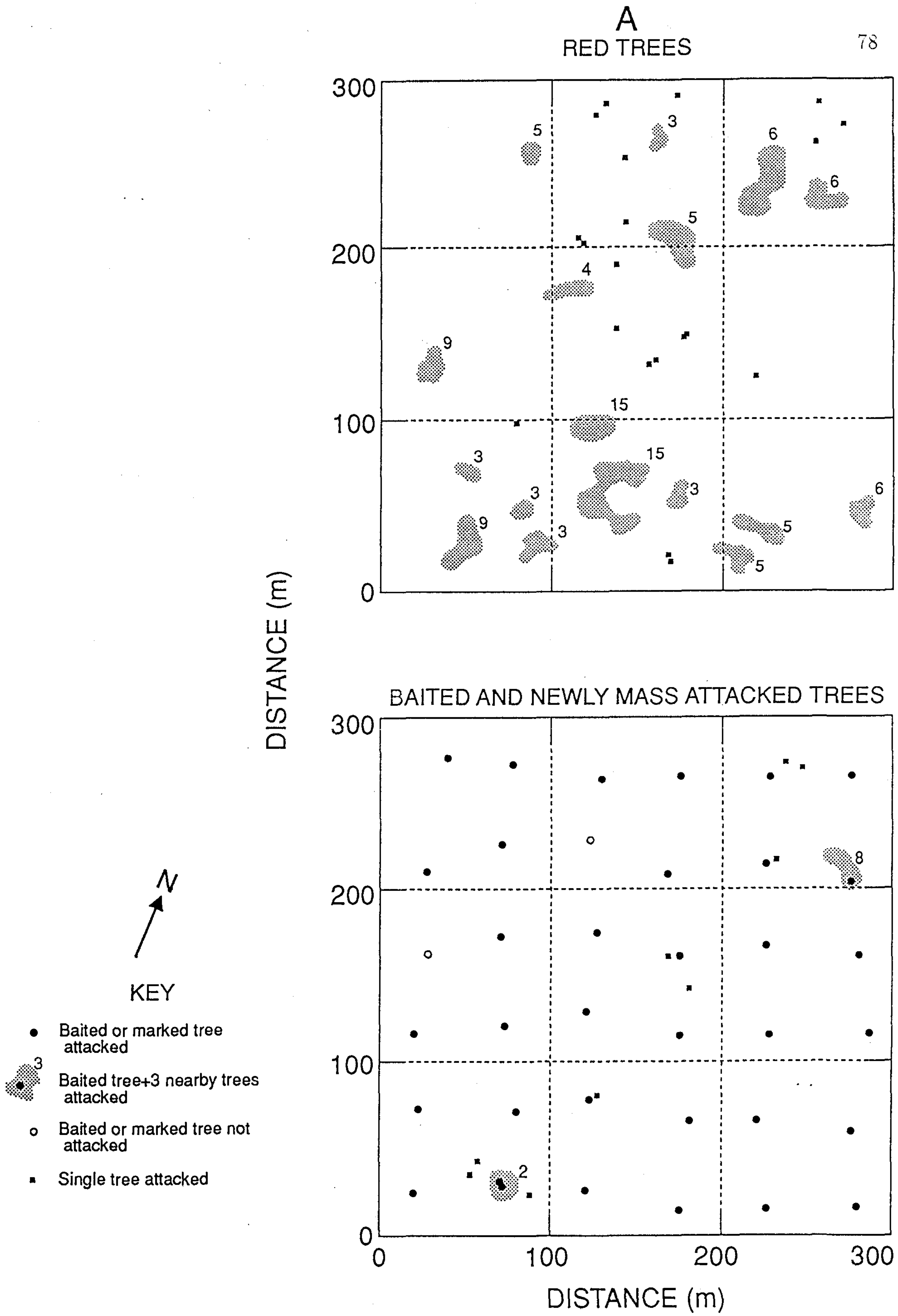

A
90
80
70
60
50
40
30
20
10
0
MASS ATTACK, BAITED BLOCKS
MASS ATTACK, CONTROL BLOCKS
RED TREES, BAITED BLOCKS
RED TREES, CONTROL BLOCKS
10
20
30
40
50
NEAREST NEIGHBOUR DISTANCE (m)
NUMBER OF NEAREST NEIGHBOURS (% OF TOTAL)
B
60
50
40
30
20
10
0
10
20
30
40
50
DISTANCE TO NEAREST MARKED OR BAITED TREES (m)

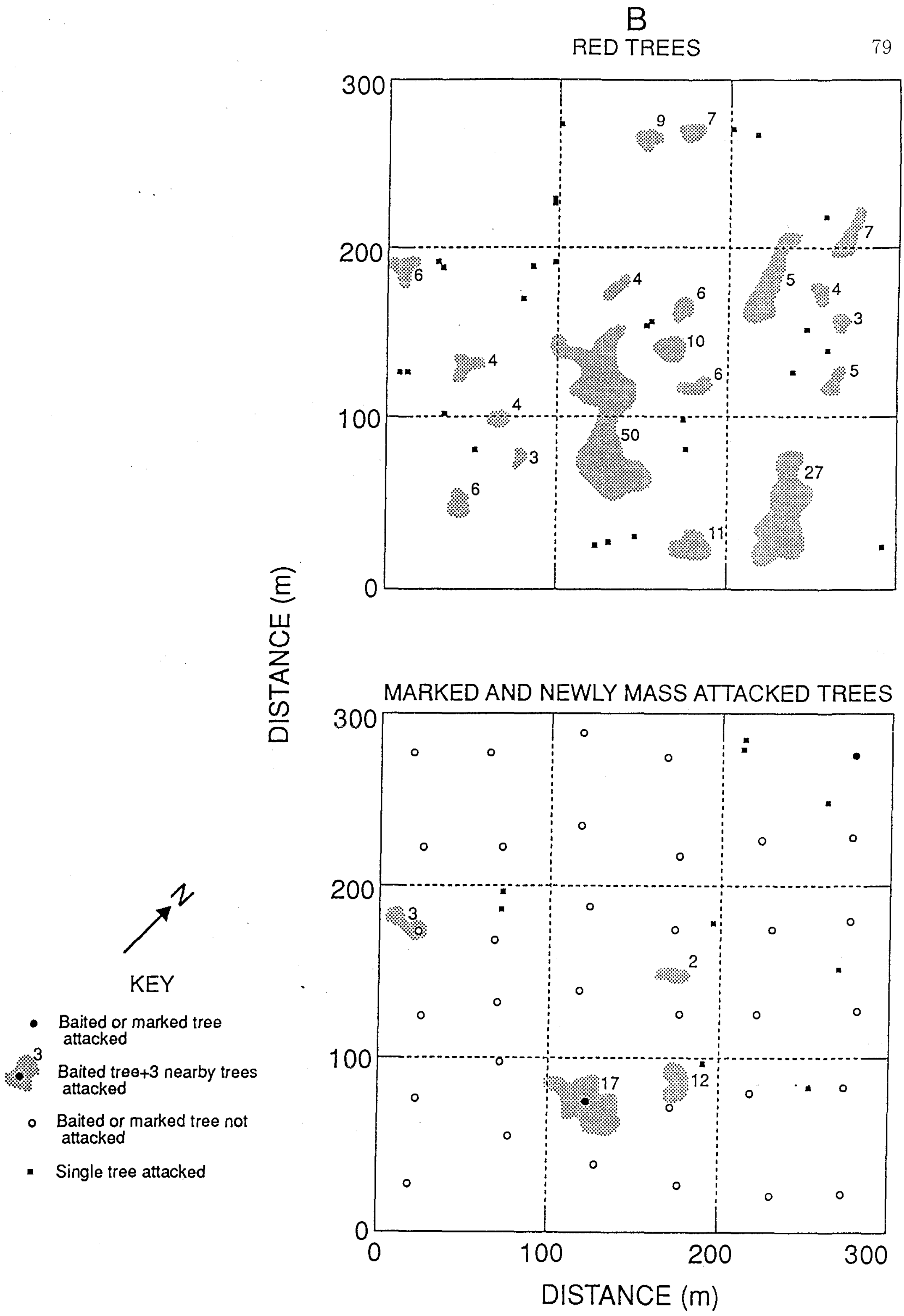
treated than in the control block, and the percentage of nearest neighbours within ≤ 10 m of each other was lower for new mass attacks in the treated blocks than in the control block. However, nearest neighbour distances of new mass attacks were approximately bimodally distributed in the baited blocks, with most nearest neighbours either ≤ 10 m apart (43.5 %), or 50 ± 10 m (29.2 %) apart (Fig. 4.3-1a). This result was different from the control block, where distribution of mass attack more closely resembled the distribution of red trees (Table 4.3-2). Similarly, a bimodal distribution is seen for distances between mass-attacked and baited trees, with most trees either 10 m (22.8 %) or 50 ± 10 m (54.7 %) from baited trees (Fig. 4.3-1b). The bimodal distribution of mass-attacked, nearest neighbour distances explains the non-aggregated distribution indicated by the Clark-Evans statistic, and suggests that the normally aggregated distribution of beetle-attacked trees was virtually eliminated. This relationship was not evident for the mean distance of red trees to baited trees for either treatment nor for mean distance of newly mass attacked trees to marked trees in the control block for which distributions approximated that of red trees (Fig. 4.3-1a, b). Baiting nearly tripled the mean distance of red trees to the nearest newly mass-attacked tree (Table 4.3-2; Fig. 4.3-2a, b).

Sixteen ha Experiment. Diameters of trees in one baited block were significantly greater than in the paired control block; the reverse occurred in another pair (Table 4.3-1).

By chance, selection of 16 ha blocks resulted in more red trees per ha in the baited blocks than in the control blocks, although the difference was not statistically significant (Table 4.3-1). This disparity did not appear to affect nearest neighbor distances of red trees, % of red tree nearest neighbors within 10 m, or red tree distance to the nearest marked or baited tree, all of which were similar between treatments for the central and peripheral zones separately, and for whole blocks (Table 4.3-3). The Clark-Evans statistic for red trees was significantly different between

Figure 4.3-2a,b. Stem maps of trees attacked by *D. confusus* in paired baited (A) and control (B) 9 ha blocks. Baited blocks with (±)-*exo*-brevicomin released at 0.4 mg/24 h applied to 1 tree/spot over a 50 m grid. Replicate no. 2, Merritt, British Columbia, 1986.


A
RED TREES
BAITED AND NEWLY MASS ATTACKED TREES
DISTANCE (m)
DISTANCE (m)
0
100
200
300
0
100
200
300
5
3
6
6
5
4
9
15
15
3
3
3
9
3
3
6
5
5
8
2
N
KEY
● Baited or marked tree attacked
3 Baited tree+3 nearby trees attacked
○ Baited or marked tree not attacked
▪ Single tree attacked


B
RED TREES
MARKED AND NEWLY MASS ATTACKED TREES
DISTANCE (m)
DISTANCE (m)
0
100
200
300
N
KEY
● Baited or marked tree attacked
3 Baited tree+3 nearby trees attacked
○ Baited or marked tree not attacked
▪ Single tree attacked
9
7
7
6
4
6
5
4
3
10
4
6
5
4
50
3
27
6
11
3
2
17
12

treatments for whole blocks, but not central zones (Table 4.3-3). The Clark-Evans statistic for red trees was strongly negative, indicating a clumped distribution ($p < 0.0001$), but was noticeably less negative in central zones than in whole blocks (Table 4.3-1). This may be an effect of scale; the pattern of clumping could appear less intense when similar nearest neighbour distances occur within smaller areas (Upton and Fingleton 1985).

There were significantly more newly mass-attacked trees/ha in the treated blocks. This was the result of intense beetle activity in the central zone; there was no significant difference between treatments in the peripheral zone (Table 4.3-3; Figs. 4.3-3a,b, 4.3-4a,b, and 4.3-5a,b). There were significantly more new mass attacks in the central zone of baited blocks (27 per ha) than in the control blocks (3 per ha) (Table 4.3-3). In total, 107 of 126 baited trees were attacked in the central zone of treated blocks, while 4 of 132 marked trees were attacked in control blocks. The percentage change was not significantly different between treatments for whole blocks. However, the percentage change was significantly greater (55.0 ± 7.5) in the central zone of baited blocks than in the central zone of control blocks (30.8 ± 7.6). Conversely, percentage change was significantly higher in the peripheral zone of control (36.1 ± 1.8) than baited (26.1 ± 4.4) blocks, suggesting a higher level of beetle activity in the peripheral zone of control blocks (Table 4.3-3).

Mean nearest neighbour distance of newly mass-attacked trees and the % of nearest neighbours $\leq$ 10 m apart were not significantly different between treatments for whole blocks. Mean nearest neighbour distance of newly mass-attacked trees was not significantly different between treatments for central zones, however the % of nearest neighbours $\leq$ 10 m apart was significantly different indicating that baiting contained new attack in tighter groups (Table 4.3-3). No bimodality was evident in the distribution of distances. The Clark-Evans statistic was significantly more negative (more aggregated)

Table 4.3-3. Analysis of the spatial pattern of trees attacked by *D. confusus* in paired baited and control 16 ha blocks, with (±)-*exo*-brevicomin baits applied to two neighbouring trees per spot over a 50 m grid in the central 4 ha of treated blocks (n=5).

Area and criteria assessed	Red trees[a]			Newly mass-attacked trees [a]		
	Baited blocks (Mean ± SE)	Control blocks (Mean ± SE)	Probability of significant difference between baited and control blocks	Baited blocks (Mean ± SE)	Control blocks (Mean ± SE)	Probability of significant difference between baited and control blocks
Whole block						
Total trees per ha	20.1 ± 5.2	9.1 ± 2.3	NS	12.4 ± 4.5	4.9 ± 1.7	*
Nearest neighbour (m)	6.0 ± 1.1	6.8 ± 0.9	NS	7.8 ± 1.6	10.0 ± 1.1	NS
% of nearest neighbours within 10 m	87.4 ± 4.8	80.8 ± 5.0	NS	83.3 ± 2.4	79.0 ± 4.1	NS
Clark-Evans statistic	-13.7 ± 1.0	-10.2 ± 0.8	*	-10.5 ± 1.5	-7.7 ± 0.3	NS
% change	-	-	-	36.6 ± 4.2	35.0 ± 1.6	NS
Nearest red tree (m)	-	-	-	18.0 ± 2.6	14.0 ± 1.5	NS
% of nearest red trees within 10 m	-	-	-	40.7 ± 6.9	52.2 ± 4.1	*
Peripheral zone						
Trees per ha	17.6 ± 4.2	9.1 ± 2.7	NS	7.4 ± 3.4	5.4 ± 1.9	NS
% change	-	-	-	26.1 ± 4.4	36.1 ± 1.8	*

Table 4.3-3 (continued). Analysis of the spatial pattern of trees attacked by *D. confusus* in paired baited and control 16 ha blocks, with (±)-*exo*-brevicomin baits applied to two neighbouring trees per spot over a 50 m grid in the central 4 ha (n=5).

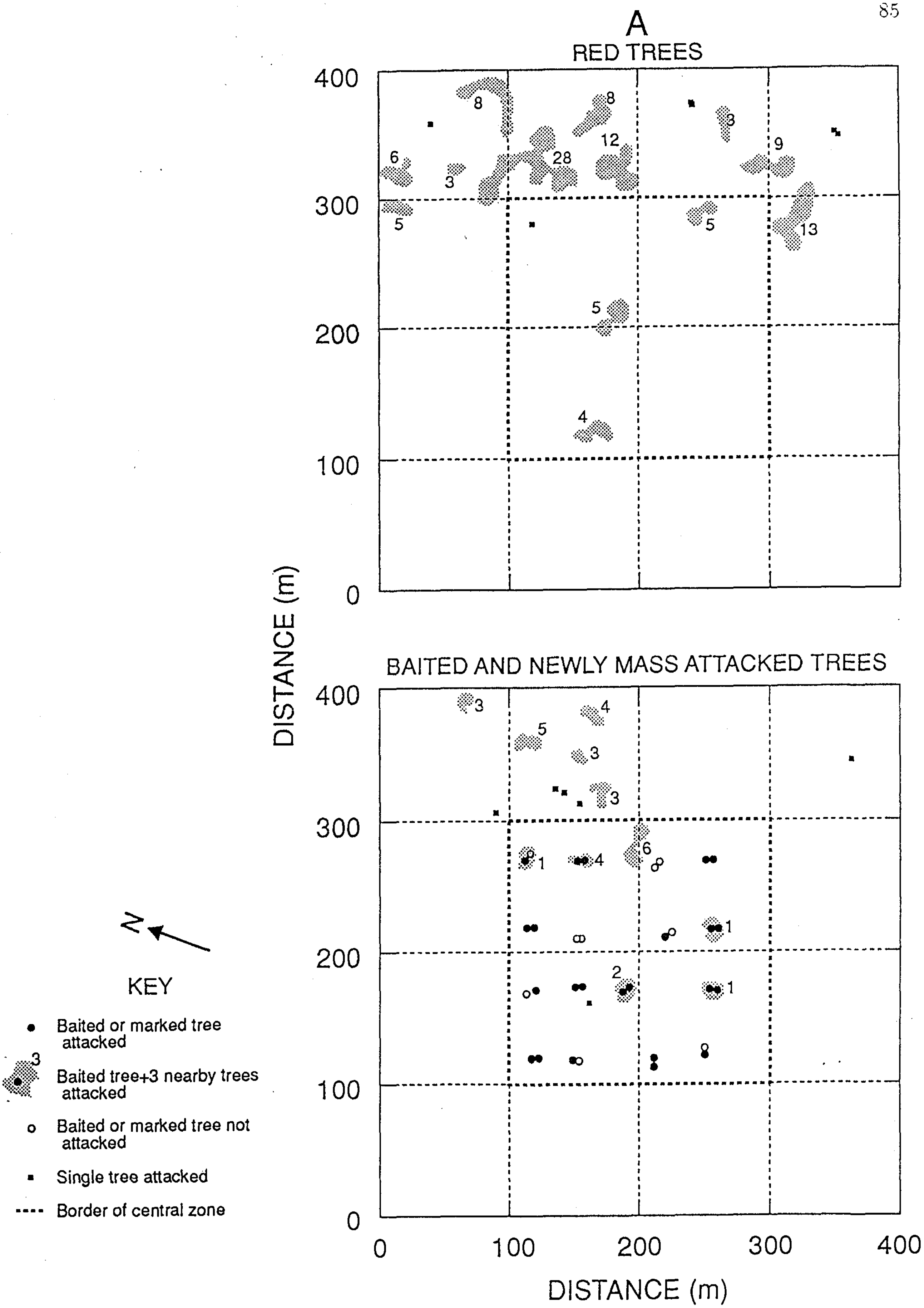
Area and criteria assessed	Red trees[a]			Newly mass-attacked trees [a]		
	Baited blocks (Mean ± SE)	Control blocks (Mean ± SE)	Probability of significant difference between baited and control blocks	Baited blocks (Mean ± SE)	Control blocks (Mean ± SE)	Probability of significant difference between baited and control blocks
Central zone						
Trees per ha	27.6 ± 9.5	9.2 ± 3.7	NS	27.4 ± 8.9	3.1 ± 1.0	*
Nearest neighbour (m)	8.0 ± 2.3	6.6 ± 0.6	NS	5.2 ± 0.5	13.2 ± 4.5	NS
% of nearest neighbours within 10 m	82.9 ± 9.8	86.1 ± 2.3	NS	89.6 ± 1.6	67.7 ± 11.3	*
Clark-Evans statistic	-7.0 ± 1.6	-5.4 ± 0.6	NS	-8.6 ± 0.1	-3.5 ± 0.6	*
% change	-	-	-	55.0 ± 7.5	30.8 ± 7.6	*
Nearest marked or baited tree (m)	18.2 ± 1.0	19.0 ± 1.3	NS	8.8 ± 0.7	15.0 ± 1.6	*
% of nearest marked or baited trees within 10 m	17.9 ± 3.7	14.3 ± 4.2	NS	74.5 ± 5.2	25.2 ± 14.0	*
Nearest red tree (m)	-	-	-	24.0 ± 4.4	13.8 ± 2.9	NS
% nearest red trees within 10 m	-	-	-	59.7 ± 10.4	77.8 ± 14.4	*

Table 4.3-3 (continued). Analysis of the spatial pattern of trees attacked by *D. confusus* in paired baited and control 16 ha blocks, with (±)-*exo*-brevicomin baits applied to two neighbouring trees per spot over a 50 m grid in the central 4 ha (n=5).

Area and criteria assessed	Red trees[a]			Newly mass-attacked trees [a]		
	Baited blocks (Mean ± SE)	Control blocks (Mean ± SE)	Probability of significant difference between baited and control blocks	Baited blocks (Mean ± SE)	Control blocks (Mean ± SE)	Probability of significant difference between baited and control blocks
Pooled data for all central zones						
No. of trees	297	136	NA	318	48	NA
Nearest marked or baited tree (m)	18.3 ± 0.5	17.8 ± 0.6	NA	5.3 ± 0.4	9.9 ± 1.6	NA
% of nearest marked or baited trees within 10 m	16.2	16.9	NA	88.7	66.7	NA
Nearest red tree (m)	-	-	-	22.4 ± 1.1	13.6	NA
% of nearest red trees within 10 m	-	-	-	28.3	48.0	NA

[a] Friedmans test (Systat 1988) used for analysis of distance and count data and Clark-Evans statistic, G-test (Zar 1984) used for comparison of percentage data. * = $p \leq 0.05$, NS = not significant, NA = no analysis computed.

Figure 4.3-3a,b. Stem maps of trees attacked by *D. confusus* in paired baited (A) and control (B) 16 ha blocks. Baited blocks with (±)-*exo*-brevicomin released at 0.8 mg/24 h applied to 2 trees/spot over a 50 m grid in the central 4 ha of block. Replicate no. 2, Merritt, British Columbia, 1987.


A
RED TREES
BAITED AND NEWLY MASS ATTACKED TREES
DISTANCE (m)
DISTANCE (m)
0
100
200
300
400
8
8
6
3
28
12
5
3
9
5
13
5
4
3
4
5
3
3
6
1
4
1
2
1
N
KEY
Baited or marked tree attacked
Baited tree+3 nearby trees attacked
Baited or marked tree not attacked
Single tree attacked
Border of central zone

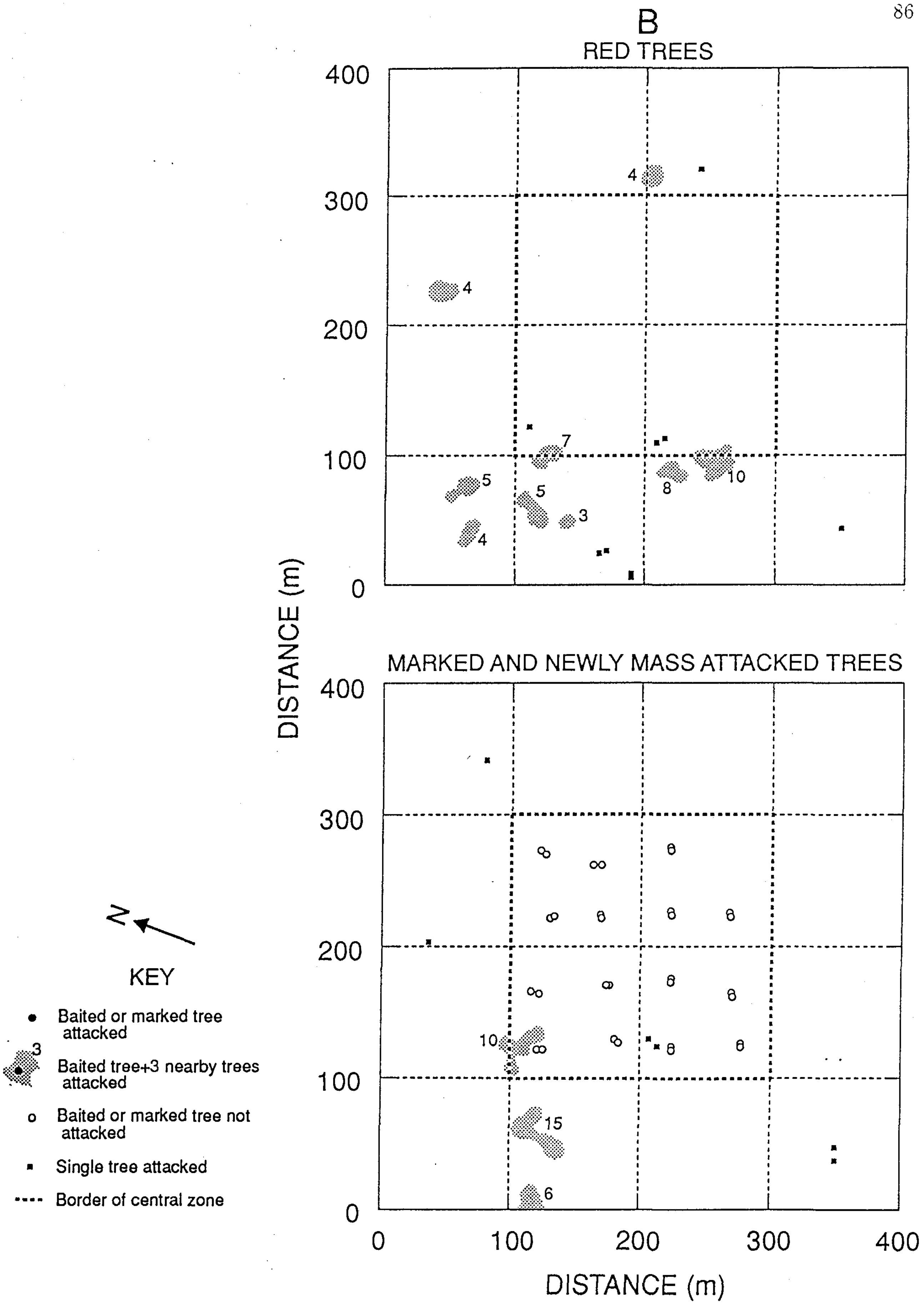
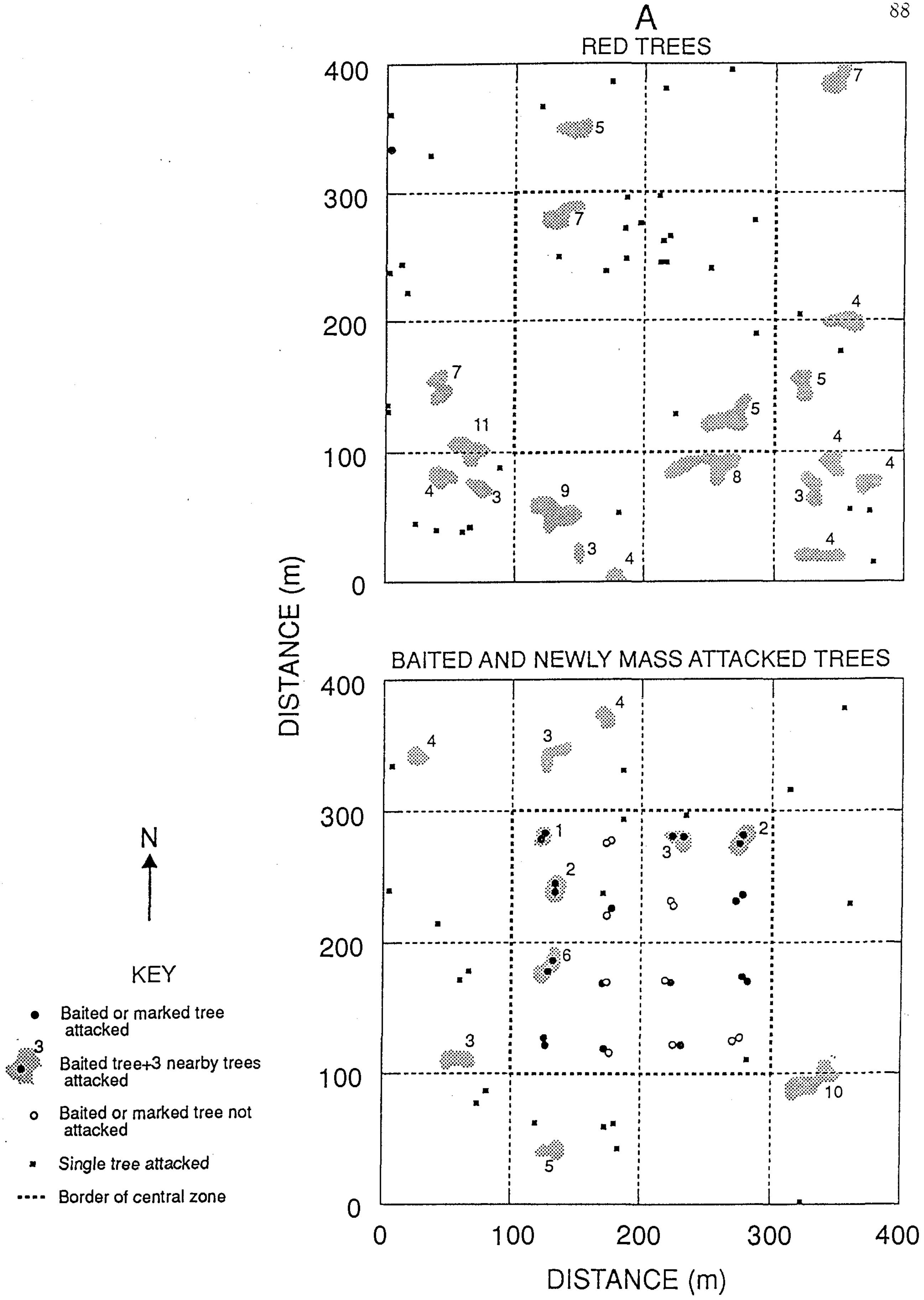

B
RED TREES
400
300
200
100
0
4
4
7
5
5
3
4
8
10
DISTANCE (m)
MARKED AND NEWLY MASS ATTACKED TREES
400
300
200
100
0
10
15
6
0
100
200
300
400
DISTANCE (m)
N
KEY
● Baited or marked tree attacked
3
Baited tree+3 nearby trees attacked
o Baited or marked tree not attacked
▪ Single tree attacked
---- Border of central zone

Figure 4.3-4a,b. Stem maps of trees attacked by *D. confusus* in paired baited (A) and control (B) 16 ha blocks. Baited blocks with (±)-*exo*-brevicomin released at 0.8 mg/24 h applied to 2 trees/spot over a 50 m grid in the central 4 ha of block. Replicate no. 1, Telkwa, British Columbia, 1987.


A
RED TREES
BAITED AND NEWLY MASS ATTACKED TREES
DISTANCE (m)
DISTANCE (m)
0
100
200
300
400
N
KEY
● Baited or marked tree attacked
3 Baited tree+3 nearby trees attacked
○ Baited or marked tree not attacked
■ Single tree attacked
---- Border of central zone
7
5
7
4
7
5
5
11
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8
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3
9
3
4
4
4
3
1
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2
6
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10
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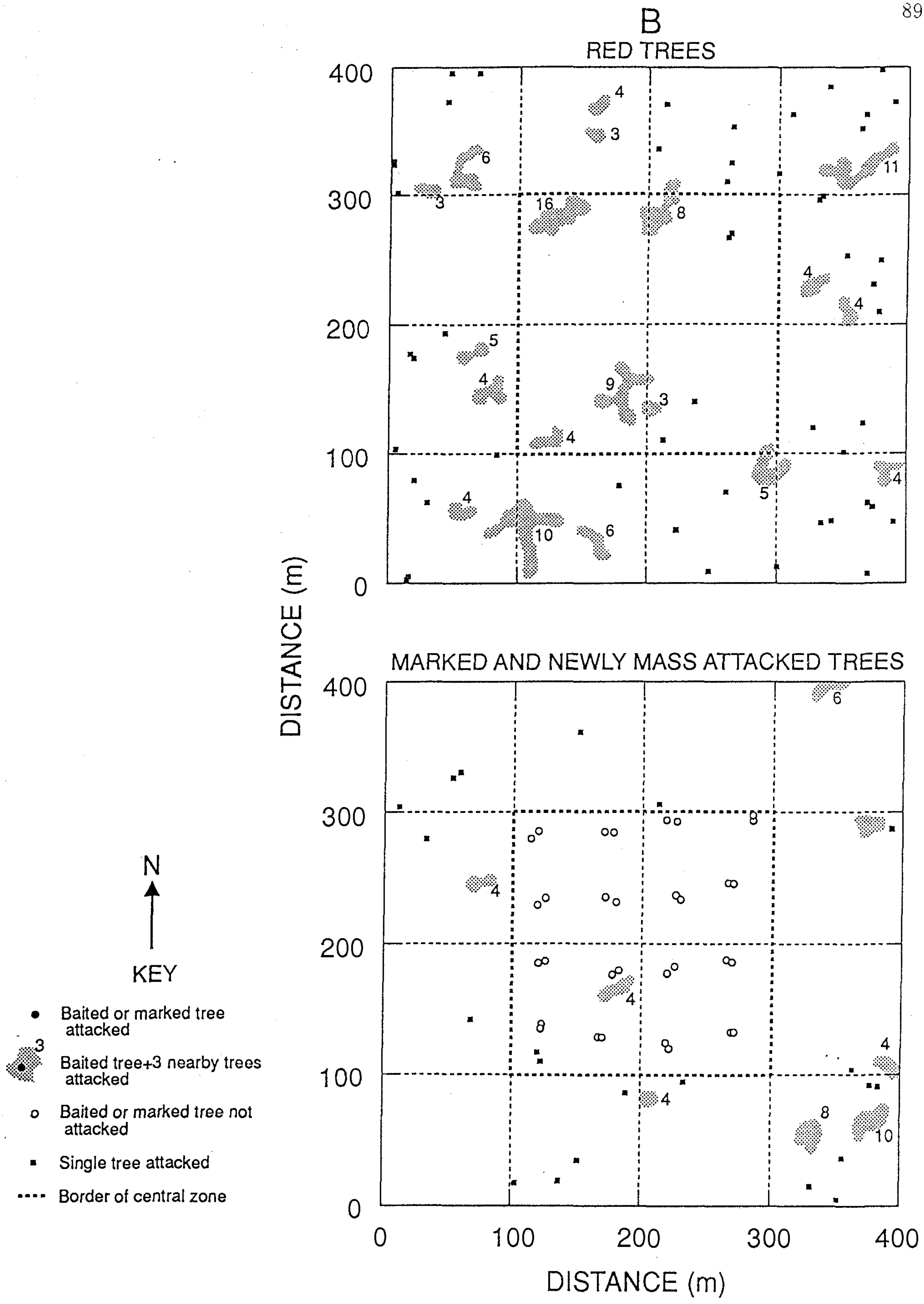
B
RED TREES
MARKED AND NEWLY MASS ATTACKED TREES
DISTANCE (m)
DISTANCE (m)
0
100
200
300
400
4
3
6
3
16
8
11
4
4
5
4
9
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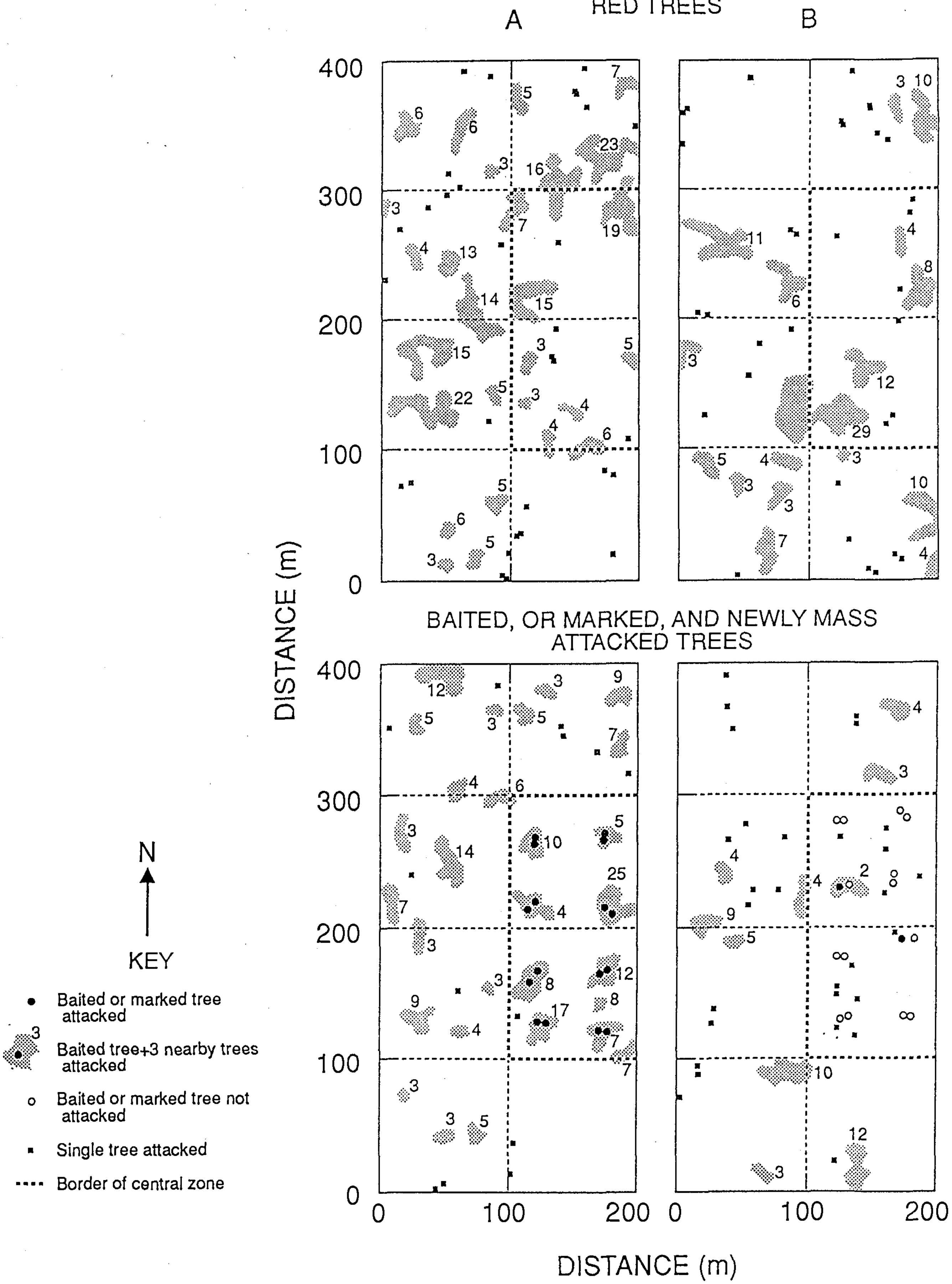
4
5
4
4
10
6
6
4
4
4
4
8
10
N
KEY
● Baited or marked tree attacked
3 Baited tree+3 nearby trees attacked
o Baited or marked tree not attacked
▪ Single tree attacked
---- Border of central zone

Figure 4.3-5a,b. Stem maps of trees attacked by *D. confusus* in paired baited (A) and control (B) 16 ha blocks, illustrating effects of treatments in stands with very high levels of *D. confusus* activity. Baited blocks with (±)-*exo*-brevicomin released at 0.8 mg/24 h applied to 2 trees/spot over a 50 m grid in the central 4 ha of block. Replicate no. 2, Telkwa, British Columbia, 1987.


RED TREES
A
B
BAITED, OR MARKED, AND NEWLY MASS ATTACKED TREES
DISTANCE (m)
400
300
200
100
0
0
100
200
DISTANCE (m)
N
KEY
● Baited or marked tree attacked
3
Baited tree+3 nearby trees attacked
○ Baited or marked tree not attacked
▪ Single tree attacked
---- Border of central zone

in the central zone of treated blocks (-8.6 ±0.1) than in the central zone of control blocks (-3.5 ± 0.6), again suggesting that baiting contained new attack intighter groups (Table 4.3-3). Location of newly mass-attacked trees in the central zone was clearly related to baiting; distance to the nearest baited or marked tree was significantly less in baited central zones (Table 4.3-3; Figs. 4.3-3a,b, 4.3-4a,b, and 4.3-5a,b). Within the central zones, there was a strong suggestion that the average distance between a red tree and the nearest newly mass-attacked tree was less in control than in baited blocks ($p = 0.655$) (Table 4.3-3). Further, the percentage of newly mass-attacked trees within 10 m of a red tree was significantly greater in the control blocks for whole blocks and central zones (Table 4.3-3).

Data for nearest neighbours were pooled for the central zone in all blocks to determine the overall distribution of newly mass-attacked trees relative to baited or marked trees. The nearest neighbour distance in baited blocks was approximately half that in control blocks, and 88.7 % of all newly mass-attacked trees were within 10 m of a baited tree, while only 66.7 % of newly mass-attack trees were within 10 m of a marked tree in control blocks (Table 4.3-3).

Impact. Diameter data for newly mass-attacked trees, red, and gray trees from control blocks of the 9 ha block experiment were compiled to estimate the volume of subalpine fir mortality. Total mortality in the 9 ha blocks was 21.7 m^3/ha, of which 8 % was in newly-massed attacked trees, 50 % in red trees, and 42 % in gray trees. Mean dbh over all blocks was similar between newly-mass attacked, red, and gray trees (32 ± 1.5 cm, 32 ± 0.5 cm, and 32 ± 0.6 respectively). Annual mortality, estimated as per Chap. 2, was 3.6 m^3/ha, which was reasonably similar to the estimate of 4.2 m^3/ha in Chap. 2. Diameter data for gray trees were not available for the 16 ha experiment. Total mortality in the 16 ha blocks was 11.8 m^3/ha, of which 34 % was in newly mass-attacked trees. Mean dbh over all blocks was again similar between newly-mass attacked and red trees (36 ± 0.6 cm and 36 ± 0.5 cm respectively).

4.3.3 Discussion

Both the 9 and 16 ha block experiments produced results indicating that the within-stand distribution of newly mass-attacked trees was strongly influenced by the use of (±)-*exo*-brevicomin baits. The apparently bimodal distribution of nearest neighbour distances for newly mass-attacked trees in the 9 ha blocks reflects the placement of baits at 50 m intervals, and an apparent lack of sufficient beetles to "spill over" onto other trees. Hence, the nearest mass-attacked neighbour to a mass-attacked, baited tree was often another baited tree (Fig. 4.3-2a, b). As a result, the Clark-Evans statistic showed a significantly weaker clumping of newly mass-attacked trees in the baited than in the control blocks. The fact that baiting greatly increased the mean distance of red trees to the nearest newly mass-attacked tree in both experiments suggests that the relationship between the locations of pre- and post-treatment beetle population centres was altered.

The relatively low levels of beetle activity in the 9 ha blocks may have been due to low efficacy of the baiting pattern, caused in part by the low release rate of (±)-*exo*-brevicomin from only 1 tree at each spot. This release rate and single tree baiting regime were selected because they had been effective in inducing attack in an earlier study. The results may also have reflected low population levels. Nevertheless, these results are a dramatic illustration of the ability of *exo*-brevicomin baits to alter attack location within stands (Figs. 4.3-2a,b, 4.3-3a,b, 4.3-4a,b, and 4.3-5a,b).

The choice of a 0.8 mg/24 h release rate on two trees per spot was based on a logical compromise that combined the results of dose-response and multiple-tree baiting experiments (Tables 3.2.1-3, 4). These data indicate that baiting shifted beetle attack patterns to centre around baited spots, and confirm the efficacy of combining the 0.8

mg/24 h release rate of *exo*-brevicomin with baiting more than 1 tree per spot. Further, application of baits to 2 trees in a spot at 50 m intervals in the 16 ha blocks resulted in a virtual duplication of the "natural" aggregated pattern, in terms of nearest neighbour distances and the Clark-Evans statistic, displayed by newly mass-attacked trees in control blocks and by red trees in all blocks. The lower percentage change in the peripheral vs. central zones of the baited 16 ha blocks suggests that intensification of attack in the central zones of baited blocks was augmented by beetles from the peripheral zones, as occurs with the mountain pine beetle (Borden *et al.* 1983, 1986; Gray and Borden 1989). Visual examination of stem maps suggests that the effect of baiting on the redistribution of new mass attack diminishes outside of the baited zone (4.3-3a,b, 4.3-4a,b, and 4.3-5a,b).

The aggregated distribution of attacked trees observed for *D. confusus* probably explains some of the variation obtained during semiochemical studies using funnel traps under the sampling regime (50 m spacing) generally employed. Funnel trap placement at 15 m intervals would help to minimize the variation introduced by the patchy distribution of beetle populations.

Comparisons of numbers of newly-attacked trees ("green attack") to previously-attacked trees ("red trees") have been used to assess containment and concentration programs for the mountain pine beetle (Borden 1990). However, as Gray and Borden (1989) point out, the assumption that an increased green to red tree ratio indicates successful containment is valid only if baiting does not cause a proportionately lighter attack on this increased number of trees. This aspect of population distribution was not examined in these experiments; however data from Table 3.2-3 suggest that baiting trees with (±)-*exo*-brevicomin released at 0.8 mg/24 h intensifies attack. In addition, use of the ratio only makes sense if red tree counts are a reasonable measure of current local beetle populations. This is not the case with *D. confusus* in subalpine fir. Dead subalpine fir trees can retain their needles for several years (possibly up to 5) (Doidge 1983), well past the time when beetles are actually in the trees. Hence numbers of red trees represent cumulative rather than current activity. Consequently, for *D. confusus*, green: red ratios, or the "percentage change" used herein can only be regarded as a very rough "indicator" of beetle population trends. This phenomenon seriously impairs assessment of activity based on red trees counted in aerial or ground surveys. A much more reliable method of red tree classification is needed; further study is essential to determine the relationship of tree condition and diameter to beetle production.

Pooled results from the 16 ha blocks suggest that because approximately 89 % of all newly mass-attacked trees were within 10 m of a baited tree, the treatment was very effective at concentrating beetle attack within stands. This clumped pattern represents powerful control of the within stand distribution of balsam bark beetle populations. The experiment included blocks in which the pre-treatment level of beetle activity was extreme (Fig. 4.3-5a,b), which might have been expected to weaken semiochemical treatment effects (McGregor 1989).

Upton and Fingleton (1985) note that detection of a particular pattern does not necessarily indicate the process that produced the pattern; however, a knowledge of the spatial pattern of organisms is obviously useful for establishing what processes might underlie the observed arrangement of organisms. There are at least three processes that can produce a clustered spatial pattern (Upton and Fingleton 1985), and the pattern discerned for the western balsam bark beetle probably has elements of all three: 1) randomly located individual "parent" points (infested trees) have offspring that are closely associated with the location of the parent. Susceptible trees adjacent to balsam bark beetle-attacked "parent" trees are often attacked; 2) "true contagion", in which the organisms represented by the points are attracted to each other, and which obviously occurs with secondary attraction; and 3) the clustering is a result of a "patchy" (heterogeneous) environment, which can indeed be produced by the sharply undulating terrain of subalpine forests, even within a 9 ha area. Clearly, these experiments indicate that management activity can exert a strong influence over the contagion produced by secondary attraction. How much influence the other two factors exert on the distribution of *D. confusus* attack within stands, and to what extent these factors can be manipulated, e.g. through stand management practices such as partial cutting (Alexander 1975; McGregor *et al.* 1987), to manage *D. confusus* populations are interesting possibilities for further research.

In general, climax species, such as subalpine fir and Engelmann or white spruce, will dominate in a forest when there are infrequent, large-scale, catastrophic disturbances such as fire, which may occur only every 400 yr (Alexander 1987; Whitmore 1989). Small gaps (≤ 0.1 ha) then become the dominant feature of canopy dynamics and these "fine scale dynamics" create a mosaic of openings and canopy cover (Spies and Franklin 1989). Veblen (1986) suggests that the coexistence of subalpine fir and Engelmann spruce is perpetuated by fine scale dynamics. The more shade tolerant subalpine fir uses its ability to colonize small gaps in the forest, which gives it a superior recruitment rate. This compensates for a higher canopy mortality rate due to a shorter life-span and thereby maintains its abundance in the canopy. Engelmann spruce maintains its relative abundance in the canopy because a lower recruitment rate is compensated for by a lower mortality rate (Veblen 1986). I hypothesize that the aggregated pattern of trees attacked by *D. confusus* plays a role in creating fine scale gap dynamics that favour establishment and/or release of the next generation of its host, suggesting a co-evolutionary relationship (Peterman 1979).

Visual examination of stem maps clearly shows that *D. confusus* attack centres do not expand and coalesce in the way that mountain pine beetle attack centres reportedly do (Safranyik *et al.* 1974) (Figs. 4.3-2 - 5). Several questions beg examination. Why do the aggregations of attacked trees appear to be so discrete? Do trees of susceptible age and/or physiology occur in groups created by small gaps in the past. Do discrete populations of beetles become less fit as host trees are consumed, in part preventing the expansion of spot infestations (Paine *et al.* 1988)? Do intra-population effects such as the rapid buildup of natural control organisms like *Beauvaria bassiana* or *Coeloides* spp. (Stock 1981; Whitney *et al.* 1984) cause spot infestations to collapse? Possibly, the occurrence of root disease, which could also produce clumps of moribund trees, affects the attack dynamics of *D. confusus*. Attack by *D. confusus* has been correlated with the occurrence of root disease. Pathocon (1987) in central British Columbia, and James and Goheen (1981) in Colorado found that 32 % and 86 %, respectively, of beetle infested subalpine fir had root diseases.

Spatial pattern has two elements, intensity, which is the variability of density from place to place, and grain, which describes the size and distribution of various levels of intensity (Pielou 1977). The Clark-Evans statistic is not suitable for describing grain, but more sophisticated techniques are available. Refined nearest neighbour analysis, for example, examines the complete distribution function of distances, and can indicate the extent to which observed distributions depart from the Poisson distribution across the entire spectrum of distances (Upton and Fingleton 1985, Kenkel 1988). The combined count-distance method, utilizing all point-to-point distances is a second-order statistic examining variation rather than mean distances (Kenkel 1988). Consequently, it offers much greater insight into important scales of spatial patterns including distance to nearest neighbour, distance where heterogeneity begins, distance where clumping becomes significant, and distance at which maximum clustering is observed (distance between clumps) (Getis and Franklin 1987). In addition, there are multi-variate techniques which can be used to measure the degree of association between two different factors such as the location of mass attack and the occurrence of root disease centres, or the location of susceptible trees in a stand (Upton and Fingleton 1985). The use of these refined methods could aid in the development of optimal placement procedures for semiochemicals, improved survey procedures based on expected patterns of attack within stands, and strengthened models of beetle population growth and dispersal.

4.4 INHIBITION OF INFESTATIONS WITH *ENDO*-BREVICOMIN

4.4.1 Materials and Methods

Felled tree experiments. Trees at 50 m intervals were selected in *D. confusus*-infested stands near Smithers, B.C. All selected trees were apparently healthy subalpine fir trees ≥ 20 cm in diameter at dbh.

Thirty trees were used in pairs for the first experiment. One of each pair was randomly selected and felled on 11 June, 1986, prior to beetle flight. The other tree was left standing. The dbh (mean ± S.E.) was 40.3 ± 1.80 cm for felled trees, and 40.9 ± 1.97 for standing trees. All trees were examined for beetle attack in late summer, 1986.

In the second experiment trees were felled at 50 m inter-tree distance in stands infested by *D. confusus* on 24 May, 1987. Ten replications of three treatments were applied in a randomized complete block design. In the first 2 treatments 2 glass capillary tubes collectively releasing (±)-*endo*-brevicomin (98.2 % purity, Phero Tech Inc., Delta, B.C.) at 0.4 mg/24 h were placed in a 400 microlitre polypropylene tube mounted in a cardboard holder (Phero Tech Inc., Delta, B.C.) were affixed to the shaded sides of trees at 2 or 5 m spacings, to a minimum diameter of 10 cm. The average number of release devices per tree were 7 and 4, respectively, for the 2 and 5 m spacings. The third treatment was an untreated control. The felled trees were examined for beetle attack in late summer, 1987.

For both experiments, attack density was sampled in 30 x 30 cm bark squares removed from the upper surface of felled trees at dbh, or from the west side at dbh on standing trees. The west side of standing trees was sampled because beetle attack is sometimes light on surfaces exposed to full sunlight (personal observations). The underside and stump of each felled tree were examined for the presence of western balsam bark beetle attack by peeling randomly selected bark sections, in order to ascertain whether or not attacking beetles were utilizing the entire available resource.

Treated block experiment. Four replicates of paired 4 ha (200 x 200 m) blocks in stands with current beetle infestations were laid out prior to beetle flight in 1987. Two replicates were located near Merritt, B.C., and 2 were located near Smithers, B.C. One block from each pair was randomly selected for experimental treatment with 100 (±)-*endo*-brevicomin release devices, which were affixed as high as possible to the north side of trees at 10 m centres, in a grid over the central ha (100 x 100 m) within each block. Four healthy subalpine fir trees ≥ 20 cm dbh were selected at 50 m centres in the central ha of both the control and treated blocks and baited with the aggregation pheromone, (±)-*exo*-brevicomin (98% purity, Phero Tech Inc., Delta, B.C.), released as above at 0.8 mg per 24 h. (±)-*exo*-Brevicomin-baited trees acted as a "challenge" to the antiaggregation pheromone to reduce beetle attack in a stand where the baited trees simulated attractive trees undergoing natural attack. All stands were 100 % surveyed in late summer 1987. The dbh and position of each tree displaying symptoms of western balsam bark beetle attack were noted and mapped. Attacked trees were separated into two attack classes as follows: red trees attacked prior to 1987, and trees showing evidence of current mass attacks, identified by boring dust and/or live brood production. The spatial distribution of attacked trees in 10 m quadrats was plotted using Sygraph (Systat 1988).

Statistical analysis. Attack density data from the second felled tree experiment were analysed by ANOVA (Number Cruncher Statistical System, 1988). Friedmans test (Systat 1988) was used to compare counts of attacked trees per ha and the G-test (Zar 1984) was used to compare percentage change between treatments. The "percentage change" was calculated as:

$$\frac{(\text{number of mass attacked trees/ha})(100)}{(\text{number of mass attacked trees/ha} + \text{number of red trees/ha}).}$$

4.4.2 Results

Felled tree experiments. All of the 15 felled trees in the first experiment were heavily attacked along the stem to a minimum diameter (mean ± S.E.) of 10.4 ± 0.80 cm. Attack density per m^2 (mean ± S.E.) at dbh was 235.6 ± 21.36. None of the standing trees was attacked. The stumps from the felled trees lived for at least one year after cutting, and remained unattacked through two flight periods.

Attack on felled trees in the second experiment was significantly reduced by *endo*-brevicomin released at both the 2 and 5 m spacings (Table 4.4-1). In addition, only 2 of 10 logs were attacked on the underside at the 2 m spacing compared to 100 % of the control logs and logs treated with release devices at 5 m (Table 4.4-1). A small mammal, probably a ground squirrel, destroyed five devices on 3 trees in each treatment. This perturbation did not seem to affect the outcome of the experiment. Cut stumps were still alive at the time of examination. Only two of 30 stumps were attacked (Table 4.4-1), and these attacks were pitched out.

Baited block experiments. There were more red trees (attacked prior to 1987) and newly mass-attacked trees per ha in the control blocks than in the *endo*-brevicomin treated blocks (Table 4.4-2), both for whole blocks, and for central and peripheral zones separately. Differences were significant except for red trees in the central zone (Table 4.4-2).

There was no difference in the percentage change between treatments for whole blocks, but significant differences occurred between treatments for separate zones. Percentage change in the central zone of control blocks averaged 66.6 %, while the change in the peripheral zone was 30.0 %, suggesting a movement of beetles towards the baited centre of the block (Table 4.4-2). A similar pattern occurred in the treated blocks, where

Table 4.4-1. Attack by *D. confusus* on freshly felled *A. lasiocarpa* at 1.3 m from root collar for 2 spacings of *endo*-brevicomin release devices affixed to the shaded side of logs (n = 10).

Treatment	Attack per m^2 bark sample (Mean ± S.E.)[a]	Percent of logs attacked on lower surface	Percent of stumps attacked
Untreated control	124.4 ± 11.78a	100	10
1 release point per 5 m	51.1 ± 17.56b	100	10
1 release point per 2 m	8.9 ± 2.67b	20	0

[a] Means within columns followed by the same letter are not significantly different, Newman-Keuls range test, $p \leq 0.05$.

Table 4.4-2. Attack by *D. confusus* in paired baited and control 4 ha blocks, with (±)-*endo*-brevicomin applied on a 10 m grid to the central ha of baited blocks, and with (±)-*exo*-brevicomin baits applied to trees on a 50 m grid in the central ha of baited and control blocks, central British Columbia, 1986 (n=4).

Area and criteria assessed	Red trees[a]			Newly mass-attacked trees [a]		
	Baited blocks (Mean ± SE)	Control blocks (Mean ± SE)	Probability of significant difference between baited and control blocks	Baited blocks (Mean ± SE)	Control blocks (Mean ± SE)	Probability of significant difference between baited and control blocks
Total trees/ha	6.7 ± 2.2	14.7 ± 6.1	*	4.0 ± 1.6	11.6 ± 2.5	*
Trees/ha, central zone	9.3 ± 5.1	19.5 ± 9.7	NS	6.5 ± 2.5	27.8 ± 8.3	*
Trees/ha, peripheral zone	5.8 ± 2.6	13.1 ± 5.0	*	3.2 ± 1.9	6.3 ± 2.9	*
% change, whole block	-	-	-	38.4 ± 7.1	47.4 ± 9.3	NS
% change, central zone	-	-	-	55.4 ± 16.1	66.6 ± 13.9	*
% change, peripheral zone	-	-	-	28.5 ± 15.0	30.0 ± 7.7	*

[a] Friedmans test (Systat 1988) used for analysis of count data, G-test (Zar 1984) used for comparison of percentage data.
* = $p \leq 0.05$, NS = not significant.

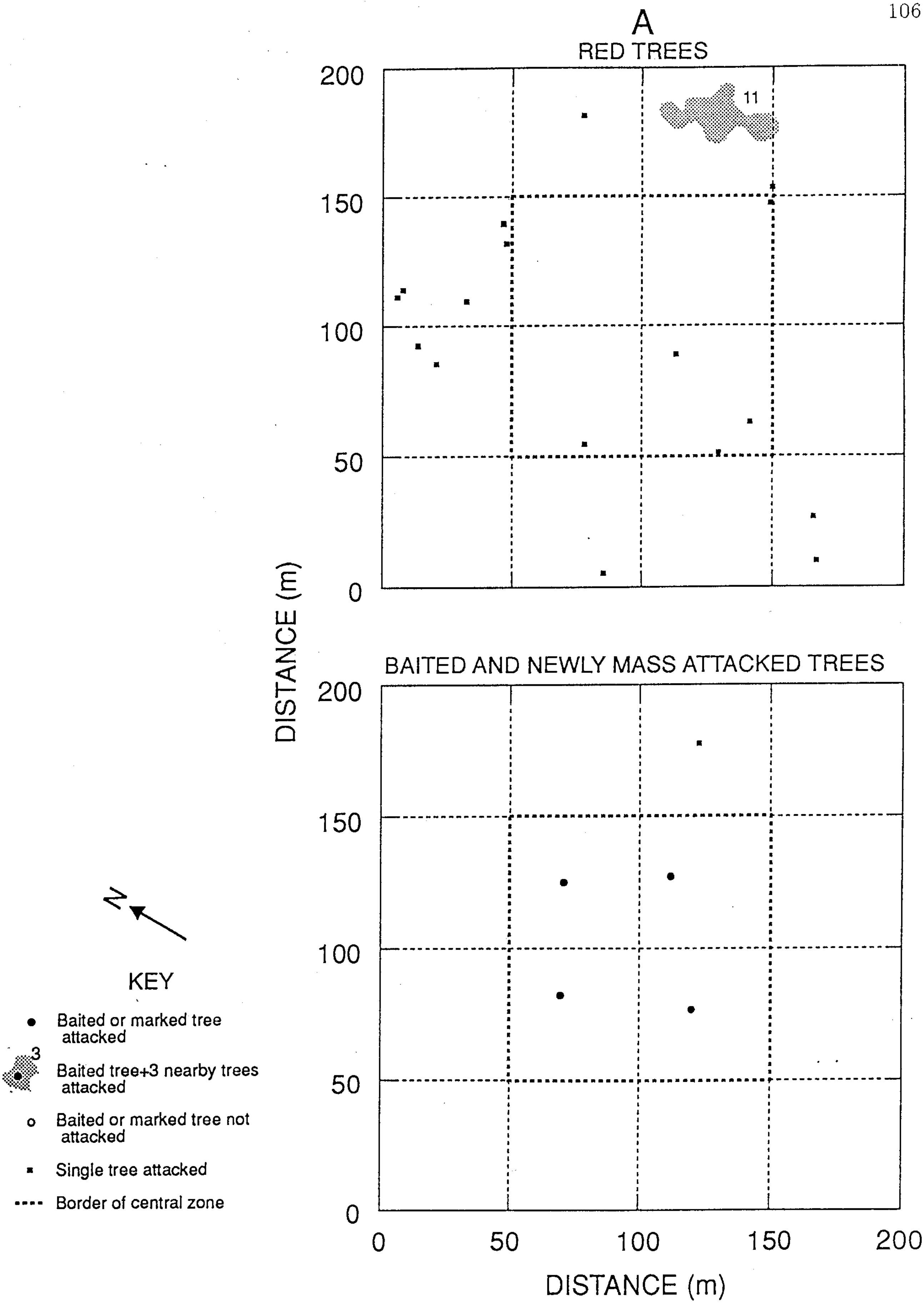
attack in the peripheral 3 ha was relatively low, possibly because of a spillover effect of the *endo*-brevicomin in the centre, or because the *endo*-brevicomin was acting synergistically with *exo*-brevicomin to bring distant beetles into the central ha where the *endo*-brevicomin acted as a close range antiaggregation pheromone.

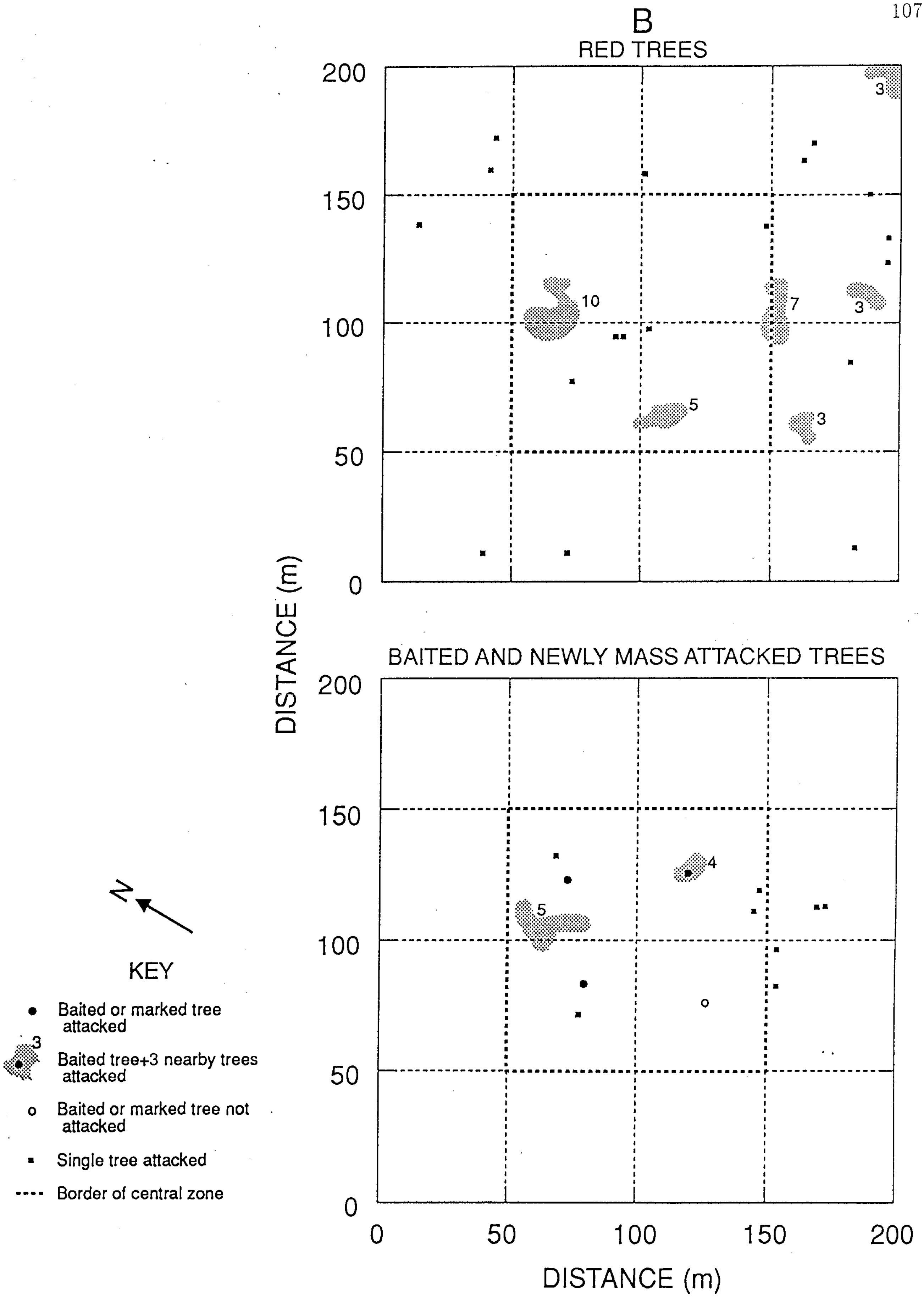
The effects of both *exo*- and *endo*-brevicomin are visually apparent in Figures 4.4-1 and 2, which are diagrammatic representations of the stand survey maps. These figures show clearly: 1) that the distribution of red trees attacked prior to 1987 was unrelated to the location of the attractive *exo*-brevicomin baits; 2) the power of the 4 *exo*-brevicomin baited trees to concentrate new attacks on and around them; and 3) the antiaggregative effect of *endo*-brevicomin in the central ha of the treated blocks. Mass attack in the central ha of the treated blocks can be seen to be limited primarily to the *exo*-brevicomin-baited trees, which demonstrates the antiaggregative effect of *endo*-brevicomin, and the ability of *exo*-brevicomin to partially override the antiaggregative effect.

4.4.3 Discussion

The results of the felled tree experiments show that *D. confusus* will readily attack freshly downed trees, and suggest that blowdown on the edge of cutblocks, or within stands after severe windstorms, may contribute substantially to population increases. They also suggest that, as for the spruce beetle (Nagel *et al.* 1957) and the Douglas-fir beetle (McMullen 1977), trap trees may be a useful component of beetle management programs. Information is required on the length of time a felled log remains attractive and suitable for colonization by beetles. Finally, results suggest that *endo*-brevicomin may be useful for reducing balsam bark beetle attack in windfall and cutblock edge blowdown. It will be important to know how attractive felled trees are to the beetle compared to standing trees baited with *exo*-brevicomin, because this comparison has a

Figure 4.4-1a, b. Stem maps of trees attacked by *D. confusus* in paired baited (A) and control (B) 4 ha blocks. Baited blocks with (±)-*endo*-brevicomin released at 0.4 mg/24 h from devices applied over a 10 m grid in the central ha. Baited and control blocks with (±)-*exo*-brevicomin released at 0.8 mg/24 h applied to 1 tree/spot over a 50 m grid in the central ha of block, Hankin Lake Replicate, British Columbia, 1987.


A
RED TREES
11
BAITED AND NEWLY MASS ATTACKED TREES
DISTANCE (m)
DISTANCE (m)
0
50
100
150
200
N
KEY
● Baited or marked tree attacked
3
Baited tree+3 nearby trees attacked
o Baited or marked tree not attacked
▪ Single tree attacked
---- Border of central zone


B
RED TREES
BAITED AND NEWLY MASS ATTACKED TREES
DISTANCE (m)
DISTANCE (m)
0
50
100
150
200
10
7
5
3
3
3
5
4
N
KEY
Baited or marked tree attacked
Baited tree+3 nearby trees attacked
Baited or marked tree not attacked
Single tree attacked
Border of central zone

bearing on how successful population manipulation can be. Dyer and Safranyik (1977) found that standing spruce trees baited with the aggregation pheromone frontalin absorbed 4 times fewer spruce beetles than unbaited windfalls. It will also be critical to know if reduced attack densities on logs (Table 4.4-1) are reflected in reduced brood production, as occurs with the spruce beetle (Lindgren *et al.* 1989).

There are probably some beetles flying through most stands near an infestation, even if there are no infested trees in the stands and most trees in a stand will be visited by bark beetles (Wood 1982; Bunt *et al.* 1980; Byers 1984; Anderbrandt *et al.* 1988). Results of the treated stand experiment (Table 4.4-2, Figs. 4.4-1,2,3) show clearly that beetles will fly through a stand and locate trees with an attractive pheromone source even when antiaggregation pheromones are present at high concentrations. This suggests that the antiaggregative effect of *endo*-brevicomin acts primarily during the landing/gallery location phase of odour orientation (Schlyter *et al.* 1987), and hence is of limited range (possibly ≤ 1m). This hypothesis is supported by the significantly different levels of attack density on logs treated with *endo*-brevicomin release devices at 2 and 5 m (Table 4.4-1). At 5 m spacings pioneer beetles attacking the treated logs either produced sufficient aggregation pheromone to partially override the antiaggregative effect of *endo*-brevicomin, and/or the beetles were not sufficiently deterred by the amount of antiaggregation pheromone present.

The baited block results do indicate that *endo*-brevicomin would be useful for protecting individual trees or small stands of high value, particularly if there are no sources of attraction within the treated area. The fate of beetles dispersing away from an infested stand treated with antiaggregation pheromone would be of concern if the beetles were simply to initiate attacks nearby (Lindgren *et al.* 1988b). Such attacks do not apparently occur around verbenone-treated spot infestations of the southern pine beetle, but this issue must be resolved for each species.

Because harvesting and intensive forest management in western Canada, and particularly in B.C., is moving into high-elevation spruce-fir stands, the impact of *D. confusus* is of increasing concern. In other areas such as the western U.S.A., *D. confusus* infestations threaten the integrity of protection forests maintained for hydrologic and aesthetic imperatives (see Chap. 1). In both situations there is a demand for reduced infestation levels, and there is a corresponding need to develop *endo*-brevicomin as an operational semiochemical. In addition, as proposed for the mountain pine beetle (Amman *et al.* 1989), the possibility of using both antiaggregation and aggregation pheromones to manipulate populations of *D. confusus* even more effectively should be investigated.

5. CONCLUSIONS

1. *Dryocoetes confusus* has been shown to be causing significant mortality in mature subalpine fir forests. In common with some other aggressive scolytids, attack is concentrated on the largest available trees. However there is no specific information available to define a susceptible tree. Further investigations are required to ascertain what factors, such as age, dbh, and associated pathogens, determine susceptibilty to balsam bark beetle attack. This information is needed before intelligent management objectives can be formulated for subalpine forests.

2. *Exo*-brevicomin is verified as an aggregation pheromone. It can be used to monitor *Dryocoetes confusus* populations. Given certain constraints, e.g. a high release rate and multiple tree baiting, it can also be used to manipulate *Dryocoetes confusus* populations.

3. *Endo*-brevicomin is shown to have antiaggregative properties. It has the potential to be used for protecting high value individual trees or small stands.

4. The aggregated nature of *D. confusus* attacks in nature, or when induced by baiting with *exo*-brevicomin, suggest the potential for exploiting small-gap stand dynamics in manipulating the beetle. Implementing small-group selective logging following the application of semiochemicals to induce small localised infestations, could directly reduce beetle populations and decrease overall stand susceptibility. Thus, a silvicutural system with a basis in pest management could be created for for subalpine fir.

5. Several phenomena require further research. Because of low catches in traps compared to other scolytid species, it is apparent that there are some components missing from the attractive pheromone blend of *D. confusus*, not the least of which may be a host volatile. It may also be that there are host volatiles which can add

significantly to the antiaggregative effect of *endo*-brevicomin. In addition, there is potential for significant variation in the components of the pheromone blend, and this must be investigated to build on the success to date, and carry the results to other areas, e.g. Alberta, the west central U.S, and perhaps even within B.C.

Possible differences in response to, and production of, semiochemicals must be investigated given the female-dominated second flight peak. This flight must be accounted for in pest management strategies, at least until its contribution to population growth is known.

A much better understanding of within-tree and within-stand population dynamics is required before accurate estimations of population levels and trends can be made. The characteristics of beetle-killed trees make this difficult. How long does a red tree contain viable brood? Does strip attack occur often, and how can it be identified? Does *D. confusus* "inoculate" trees with *C. dryocoetidis* before a successful mass attack can occur? Is there a significant interaction between root diseases and/or drought and bark beetle attack? Can semiochemical-baited traps be utilized to estimate population levels?

In many ways, subalpine forests represent the "last frontier" of forest management in B.C. Their special combination of productivity, fragility, and beauty is unique, and presents challenges requiring new perspectives and demanding a willingness to use fresh approaches. It is my hope that this thesis contributes in some small way toward that end.

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Appendix I

Table AI-1. List of insect species cited in text.

Species	Order: Family	Common Name
Apis mellifera L.	Hym: Apidae	honey bees
Choristoneura biennis Freeman	Lep.: Tortricidae	two-year spruce budworm
Choristoneura fumiferana Clemens	Lep.: Tortricidae	eastern spruce budworm
Cryptolestes turcicus (Grouvelle)	Col: Cucujidae	flour mill grain beetle
Dendroctonus frontalis Zimmerman	Col.: Scolytidae	southern pine beetle
Dendroctonus ponderosae Hopkins	Col.: Scolytidae	mountain pine beetle
Dendroctonus pseudotsugae Hopkins	Col.: Scolytidae	Douglas-fir beetle
Dendroctonus rufipennis (Kirby)	Col.: Scolytidae	spruce beetle
Dryocoetes affaber (Mannerheim)	Col.: Scolytidae	
Dryocoetes autographus (Ratzeburg)	Col.: Scolytidae	
Dryocoetes confusus Swaine	Col.: Scolytidae	western balsam bark beetle
Dryocoetes hectographus Reitter	Col.: Scolytidae	
Gnathotricus sulcatus (LeConte)	Col.: Scolytidae	
Ips avulsus Eichoff	Col.: Scolytidae	
Ips calligraphus Germar	Col.: Scolytidae	
Ips pini (Say)	Col.: Scolytidae	pine engraver
Ips typographus L.	Col.: Scolytidae	European spruce bark beetle
Scolytus multistriatus (Marsham)	Col.: Scolytidae	smaller European elm bark beetle

Table AI-2. List of scolytid semiochemicals cited in text.

Common name	Systematic name
3-caren-10-ol	7,7-dimethylbicyclo [4.1.0] hept-3-en-4-ylmethanol
endo-brevicomin	*endo*-7-ethyl-5-methyl-6,8-dioxabicyclo [3.2.1] octane
exo-brevicomin	*exo*-7-ethyl-5-methyl-6,8-dioxabicycl o[3.2.1] octane
frontalin	1,5-dimethyl-6,8-dioxabicyclo [3.2.1] octane
MCH	3-methylcyclohex-2-en-1-one
myrtenol	4,6,6-trimethylbicyclo [3.1.1]hept-3-en-10-ol
alpha-pinene	6,6-dimethylbicyclo [3.1.1] hept-2-ene
beta-pinene	6,6-dimethylbicyclo [3.1.1] hept-2(10)-ene
seudenol	3-methyl-2-cyclohexen-1-ol
trans-pinocarveol	*endo*-6,6-dimethylbicyclo [3.1.1] hept-2(10)-en-3-ol
trans-verbenol	*endo*-4,6,6-trimethylbicyclo [3.1.1] hept-3-en-2-ol
2-*p*-menthen-7-ol	*cis*- and *trans*-*p*-menth-2-en-7-ol
verbenone	4,6,6-trimethylbicyclo [3.1.1] hept-3-en-2-one

Table AI-3. List of tree species cited in text.

Species	Order: Family	Common Name
Abies lasiocarpa (Hook.) Nutt.	Coniferales: Pinaceae	subalpine fir
Picea engelmanii Parry	Coniferales: Pinaceae	Engelmann spruce
Picea glauca (Moench) Voss.	Coniferales: Pinaceae	white spruce
Pinus contorta var *latifolia* Engelm.	Coniferales: Pinaceae	lodgepole pine

Appendix II

LOTUS 1-2-3 (R) MACRO PROGRAM TO CACULATE NEAREST NEIGHBOUR DISTANCES AND THE CLARK-EVANS STATISTIC.

The following displays a sample of the output generated by a program written to calculate the Clark-Evans statistic (Clark and Evans 1957), with corrections for edge effect by Donnelly (1978), and a listing of the program code.

Sample output from program:

```
THIS PROCEDURE CALCULATES THE CLARK-EVANS (DONNELLY) STATISTIC
   based on Diggle (1981), and Upton and Fingleton (1985).
   Enter the data, and press alt-/b to start the program.

   ENTER DATA IN COLUMNS A AND B, STARTING AT A10.

   COORDINATES      LIST OF  NEAREST
      X        Y  DISTANCESNEIGHBOUR                 VARIABLE LIST
              108.8668
   89.52715 119.4257 112.3490 16.67029               POINTS        10
   118.0656 163.6906 155.2907 52.66714               COUNT1        10
   179.3033 18.33342 71.43752 17.33603               POINTX   108.5191
   83.72397 103.7981 98.28367 16.67029               POINTY   8.693611
   183.4741 1.506585 75.29870 17.33603               RMAX     115.4700
   163.2885 116.4470 120.8738 35.23319               START    10:00:00
   198.1544 111.3727 136.2992 35.23319               STOP     10:00:45
   186.7077 58.38009 92.64014 40.72543               ELAPSED  00:00:45
   45.80310 27.24975 65.40365 65.40365               MAXX          200
   108.5191 8.693611          65.40365               MAXY          200
                                                     AREA        40000
                                                     PERIMETER     800
                                                     E(NN)    36.77200
                                                     VARNNBAR6.844025
                                                     NNBAR    36.26789
                                                     CED      -0.07365
```

Listing of code for macro program to calculate nearest neighbour distances and the Clark-Evans statistic.

```
K20: 'MASTER MACRO (/C)
K21: 'sets data range
K22: 'counts no. of observations
K23: 'computes nearest neighbour for each
K24: ' element in data set
K25: (D8) '/xnENTER THE MAX X VALUE OF THE AREA   ~MAXX~
K26: '/xnENTER THE MAX Y VALUE OF THE AREA   ~MAXY~
K27: '{goto}u30~
K28: '{windowsoff}
K29: '{paneloff}
K30: '/wgra
K31: '{let start,@now}~/rfdt3start~
031: 'start time
K32: '/renndists~
K33: '{onerror j24}~
033: 'traps eror if no data range exists
K34: '/rnddata~
034: 'deletes data range
K35: '{goto}a10~
035: 'goes to top of data
K36: '/rncdata~{end}{down}{right}~
036: 'creates range data
K37: '{let SIZE,@ROWS(DATA)}
037: 'counts rows in data (=#points)
K38: '{onerror j25}~
038: 'traps error
K39: '/redistlist~
K40: '{onerror j24}~
K41: '/rnddistlist~
041: 'erases old distlist
K42: '{goto}c10~/rncdistlist~{down size-1}~
K43: '{goto}a10~
043: 'back to top of data
K44: '{for COUNT1,0,SIZE-1,1,k56}~
044: 'starts loop 1 (centre points)
K45: '{onerror j30}
045: 'traps error if no nndist range
K46: '/rndnndists~
046: 'deletes rangename nndist
K47: '{goto}d10~
047: 'goes to top of nearest distances data
K48: '/rncnndists~{end}{down}~
048: 'creates range nndist
K49: '{let NNBAR,@avg(NNDISTS)}
K50: '{let stop,@now}~/rfdt3stop~
050: 'stop time
K51: '{let elapse,(stop-start)}~/rfdt3elapse~
K52: '{windowson}
K53: '{panelon}
```

```
K55: 'CENTRE POINT LOOP (1)
K56: '/c~POINTX~{right}~
N56: 'copies X to POINTX
K57: '/c~POINTY~
N57: 'copies Y to POINTY
K58: '/cc9~distlist~
N58: 'copies sqrt fromula to distlist
K59: '{right}/re~
K60: '{right}@min(distlist)~
N60: 'min of distlist
K61: '/rv~~
N61: 'values new nndist
K62: '{down}{left 3}~
K63: '{return}~
```

```
H8: 'VARIABLE LIST
H10: 'POINTS
I10: 25
H11: 'COUNT1
I11: 6
H12: 'POINTX
I12: 47.716003819
H13: 'POINTY
I13: 27.89932061
H14: 'RMAX
I14: @SQRT(AREA/3)
H15: 'START
I15: (D8) 33100.670405
H16: 'STOP
I16: (D8) 33100.667778
H17: 'ELAPSED
I17: (D8) 0.0005092593
H18: 'MAXX
I18: 58.5
H19: 'MAXY
I19: 58.5
H20: 'AREA
I20: (G) +MAXX*MAXY
H21: 'PERIMETER
I21: (G) 2*(MAXX+MAXY)
H22: 'E(NN)
I22: 0.5*(@SQRT(AREA/SIZE))+0.0514*PERIMETER/SIZE+
      0.041*PERIMETER/SIZE^(3/2)
H23: 'VARNNBAR
I23:
      (@SQRT(0.0703*AREA+0.037*PERIMETER*@SQRT(AREA/SIZ
      E)))/SIZE
H24: 'NNBAR
I24: 23.507421825
H25: 'CED
I25: (NNBAR-ENN)/VARNN
```